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- 1-3. Abrolhos Amphipoda and Isopoda.  
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## E R R A T A.

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### Page

- 47, line 21, for Thiers, read Miers.  
 219, „ 6, read *Robinia Pseudo-Acacia*.  
 243, „ 7 from bottom, for *Pentanogaster* read *Pentagonaster*.  
 288, „ 30, read extremely.  
 545, „ 8  
 577, „ 17 } read DAKINI.  
 578, „ 40 }

### *Addenda to "The Foraminifera of Lord Howe Island."*

Page 632, after line 12, insert

156 a. *DISCORBINA DIMIDIATA* *Parker & Jones*.

*Discorbina dimidiata* Carpenter, Parker & Jones, 1862, ISF. p. 201, fig. 32 n.

„ „ Parker & Jones, 1865, NAAF. pp. 385 & 422, pl. 19.  
 fig. 9.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 698.

Frequent. The specimens are rather smaller than those characteristic of Australian shore-sands, but are quite typical.

Page 636, before line 13 from bottom, insert

175 a. *PULVINULINA MENARDII* (*d'Orbigny*).

*Rotalia menardii* d'Orbigny, 1826, TMC. p. 273, no. 26, Modèle no. 10.

*Pulvinulina* „ Brady, 1884, FC. p. 690, pl. 103. figs. 1, 2.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 715.

A single small pelagic specimen.

Plates 27, 28, in legend read OPISTHOBRANCHIATA.





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THE PERCY SLADEN TRUST EXPEDITIONS\* TO THE ABROLHOS  
ISLANDS (INDIAN OCEAN).

Under the Leadership of Prof. W. J. DAKIN, F.L.S., F.Z.S.

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Amphipoda and Isopoda. By W. M. TATTERSALL, D.Sc., Keeper of the  
Manchester Museum. (Communicated by Prof. W. J. DAKIN, F.L.S.)

(PLATES 1-3.)

[Read 5th May, 1921.]

I AM indebted to Professor Dakin for the opportunity of examining the small collection of Amphipoda and Isopoda which he made during his expedition to the Abrolhos Islands. Nine species of Amphipoda and three of Isopoda were found in the collection. The number of specimens was very small, and considerable difficulty has been encountered in the endeavour to identify them satisfactorily. I have not been able to satisfy myself that any of the Amphipoda represent undescribed species, but in almost all cases the specimens showed some departure from existing descriptions. The recent work of Chilton has, however, shown that in the Amphipoda we are dealing with a dominant and virile group of Crustacea exhibiting relatively endless variations, and the time has now arrived when it is better to determine the extent of specific variation than to regard each departure from the normal as of specific value. Future work will undoubtedly reduce the number of valid species of Amphipoda.

\* Acknowledgement must be made here also of a grant from the Government Grant Committee of the Royal Society, and a grant from the British Association.

The main interest of the collections lies in the bearing which it has on the general question of the origin of the fauna of the Abrolhos Islands. As Professor Dakin has already pointed out, these islands are remarkable as being the most southerly islands in the world with coral reefs fringing their shores, and this fact would suggest that the fauna of the islands should, in the main, bear a strong tropical facies. The Amphipoda in this collection bear out that suggestion. I have in the following table indicated the known geographical distribution of all the species in the collection. It will be seen at once that six of them have a wide distribution in the tropical and sub-tropical waters of the Indian and Western Pacific Oceans, ranging from South and East Africa to the Oceanic Islands of the Pacific. Two other species, *Parharpinia villosa* and *Grubia setosa*, have so far only been met with in the waters round South and East Australia and New Zealand. Only one species, *Parawaldeckia kidderi*, seems to be a migrant from the Southern waters of the Antarctic sub-Polar seas.

Of the Isopoda, two species are described as new, but all three species in this collection belong to the Sphæromidæ, a family of Isopoda characteristic of the warmer waters of the globe.

	South Africa.	East Africa. Red Sea.	Indian Ocean, Ceylon, Seychelles, Maldives.	Tropical Australia, Torres Straits, etc.	Australia and Tasmania.	Tropical and sub-tropical Isles of Pacific.	New Zealand.	Sub-Antarctic Isles of New Zealand.	Other localities.
<i>Parawaldeckia kidderi</i> . . . .	..	..	..	×	×	×	×	×	Kerguelen.
<i>Parharpinia villosa</i> . . . . .	..	..	..	..	×	..	×	..	..
<i>Leucothoë spinicarpa</i> . . . .	×	×	×	×	×	..	..	..	..
<i>Ceradocus rubromaculatus</i> . .	×	×	×	×	×	×	×	..	..
<i>Mæra tenella</i> . . . . .	..	..	×	..	..	×	..	..	..
<i>Mæra mastersii</i> . . . . .	×	×	..	×	×	×	×	..	..
<i>Elasmopus subcurinatus</i> . . .	×	..	×	..	×	..	×	..	..
<i>Eurysetheus atlanticus</i> . . .	×	..	×	..	×	..	..	..	Cape Verde.
<i>Grubia setosa</i> . . . . .	..	..	..	..	×	..	..	..	..
	Stebbing, 1908. Bernard, 1916.	Walker, 1909. Bernard, 1916.	Walker, 1904, 1905, 1909.	Miers, 1884.	Stebbing, 1910. Haswell, 1880. Chilton, 1916.	Chevreaux, 1908. Chilton, 1910. Dana, 1852.	Chilton, 1916. Thomson.	Chilton, 1909.	

## AMPHIPODA.

## Family LYSIANASSIDÆ.

Genus PARAWALDECKIA, *Stebbing*.1. PARAWALDECKIA KIDDERI (*S. I. Smith*). (Pl. 1. figs. 1-6.)

*Nannonyx kidderi*, Chilton, 1909, p. 615.

*Parawaldeckia thomsoni*, Stebbing, 1910 (1), p. 571.

*Locality*. Dredge off Wallaby Group, one male and two females, 6-7 mm.

*Distribution*. Kerguelen (Smith), Torres Straits (Miers), Tasmania (Thomson), New Zealand (Thomson), Campbell Islands and Auckland Islands (Chilton), Kermadec Islands (Chilton).

*Remarks*. The difficulties which present themselves to the student of Amphipoda in attempting to identify isolated specimens from remote localities are nowhere more abundantly illustrated than by a reference to the history of this species, as detailed by Chilton in the paper quoted above. It had been referred to three different genera and been described under at least five and probably as many as eight different specific names. Its adventurous career was even then not at an end, for in the next year Stebbing, who had not been able to consult Chilton's paper before his own went to press, proposed a new genus, *Parawaldeckia*, for the reception of *Nannonyx thomsoni*, one of the many synonyms of this species. It seems that at last the species has a permanent abiding place of its own.

I believe my specimens to belong to the species as described by Chilton. They agree closely with his description except in one point. The adult male presents the usual sexual differences in the third uropods exhibited by so many Lysianassidæ, in having the rami of these appendages enlarged and fringed with plumose setæ. Chilton says that in the male the third uropods are the same as in the female. I give a figure of the telson of one of my specimens, showing it to be slightly excavated but not distinctly cleft. Each lobe of the apex is armed with two short spines, and there are two delicate plumose setæ on each lateral margin. In this respect my specimens are in substantial agreement with Chilton's descriptions. The outer plate of the maxilliped is broadly rounded and unarmed, the inner plate truncate and armed with three blunt teeth.

The genus *Parawaldeckia* is characterised by the possession of accessory lobes to the branchial vesicles and by having the last joint of the peduncle of the second antenna of the male dilated and moderately long, the remaining joints being small. It is very closely allied to *Waldeckia*, and differs only in having the telson slightly excavated, whereas in *Waldeckia* it is deeply cleft. My specimens agree with the definition of the genus *Parawaldeckia* in these points. There can be no question as to its relationship to *Waldeckia*, for a

comparison of the figures of some of the appendages given herewith with those published by Chevreux and Walker for *Waldeckia* will show the closest agreement in general form, especially in the first and second gnathopods.

### Family PHOXOCEPHALIDÆ.

#### Genus PARHARPINIA, Stebbing.

#### 2. PARHARPINIA VILLOSA (*Haswell*). (Pl. 1. figs. 7-14.)

*Phorus villosus*, Haswell, 1880 (1), p. 258, pl. ix. fig. 2.

*Parharpinia villosa*, Stebbing, 1906, p. 117.

*Locality.* Sandy Island, Wallaby Group, one female with incubatory lamellæ, 6 mm.

*Distribution.* Coasts of Australia (*Haswell*) and New Zealand (*Thomson*).

*Remarks.* In comparing this specimen with Stebbing's description, it is found to differ in the following points:—

		Stebbing.	Present specimen
1.	Antenna 1. Flagellum.	13 joints.	10 joints.
	Accessory App.	10 joints.	7 joints
2.	Antenna 2. Flagellum.	17 joints.	11 joints.
3.	Outer plate of Maxillipeds.	Extend to more than half-way along the long second joint of the palp, and are fringed with a dozen graduated spines serrate on both edges.	Barely extend beyond the first joint of the palp and have only eight serrate spines.
4.	Gnathopod 2.	Fifth joint about as long as the sixth	Fifth joint much shorter than the sixth
5.	Pereopods 1 & 2.	Apical spine of the fifth joint nearly as long as the sixth joint.	Apical spine of the fifth joint half as long as the sixth joint.
6.	Pereopod 3.	Fifth joint scarcely longer than the sixth.	Sixth joint longer than the fifth
7.	Pereopod 5.	Second joint not produced to end of fourth.	Second joint produced to end of fourth.
8.	Uropod 2.	Peduncle fringed with ten outstanding spines.	Peduncle with only eight spines.

The most important of these differences are numbers 3 and 4. The length of the outer plate of the maxillipeds is one of the characters used by Stebbing to separate the genera *Parharpinia* and *Pontharpinia*. In the former it is described as elongate and fringed with serrate spines on the inner margins. In the latter it is simply described as short. In my specimen, the maxillipeds do not appear to differ markedly from those of the genus *Pontharpinia*, except that the spines on the inner margin of the

outer plate are serrate on both margins, a feature not, so far as I aware, described in *Pontharpinia*.

I am quite unable to understand Stebbing's description of the second gnathopod unless, indeed, by some chance the descriptions of gnathopods 1 and 2 have become inadvertently transposed in his diagnosis. As will be seen from the figures of these appendages given here, the fifth joint is decidedly larger in gnathopod 1 than in gnathopod 2, and with this supposition, Stebbing's description of the gnathopods would apply to my specimen.

Stebbing's description is based on specimens from New Zealand recorded by Thomson (1882) as *Phoxus batei*, Haswell. Stebbing identifies Thomson's specimens with *Phoxus villosus*, Haswell, and refers Haswell's *P. batei* to *Pontharpinia rostrata* (Dana). On comparing my specimen with Thomson's description and figures, I find the most complete agreement except that the carpus of the second gnathopods is distinctly shorter than Thomson shows. Thomson does not describe or figure the fourth peræopods.

My specimen differs from Haswell's original description in the larger size of the eyes, in the fewer joints in the accessory appendage of antenna 1, and in the shape of the second joint of the fifth peræopods. In the characters of the eyes and the fifth peræopods it agrees with Haswell's description of *Phoxus batei*, and as the latter is said by Haswell to differ from *P. villosus* in the larger size of the eyes and the form of the fifth peræopods, it looks as if my specimen really belonged to *Phoxus batei*, Haswell = *Pontharpinia rostrata* (Dana). But the long and slender form of the fourth peræopods agrees much more with those figured by Haswell for *P. villosus*.

The genera *Pontharpinia* and *Parharpinia* are distinguished, according to the definitions of these genera given by Stebbing in 'Das Tierreich.' by the following characters :—

- (1) In *Pontharpinia* the third joint of the mandibular palp is shorter than the second. In *Parharpinia* the third joint is longer than the second.
- (2) In *Pontharpinia* the outer plates of the maxillipeds are short. In *Parharpinia* they are elongate and fringed with serrate spines on the inner margins.
- (3) In *Pontharpinia* the fourth and fifth joints of the third and fourth peræopods are expanded. In *Parharpinia* they are not expanded.
- (4) In *Pontharpinia* the expanded second joint of the fifth peræopods is greatly produced, while in *Parharpinia* it is only moderately produced.

These differences appear to me of doubtful value. My specimen is a *Parharpinia* in the characters of the mandibular palp and the form of the third and fourth peræopods, and a *Pontharpinia* in the characters of the maxillipeds and of the fifth peræopod.

On the whole, my specimen agrees most closely with those described by Thomson as *Phorus batei*. As these specimens formed the basis of Stebbing's description of *P. villosa*, Haswell, and were those upon which Stebbing founded the genus *Parharpinia*, I here record the present specimen as *Parharpinia villosa* (Haswell), with an expression of doubt as to the separate identity of the genera *Parharpinia* and *Pontharpinia*.

My specimen differs from *Pontharpinia uncinata*, Chevreux, in the evenly rounded epimeral plate of the third segment of the pleon, from *P. stimpsonii*, Stebbing, in the shorter and evenly rounded rostrum, and from *P. pinguis* (Haswell) in the less robust peræopods. I should have been quite content to record my specimen as *Pontharpinia rostrata* (Dana) except for the longer and more slender fourth peræopods. In Dana's figure the eyes are larger and more rounded in form and the rostrum shorter than in my specimen, but these differences disappear in the light of Haswell's description of *Phorus batei*, which Stebbing regards as synonymous with *P. rostrata*.

A redescription of Australian and New Zealand species is a necessity before they can be placed on a sound basis, and it is to be hoped that this will be attempted by some one on the spot who has access to material.

#### Family LEUCOTHOIDÆ.

##### Genus LEUCOTHOË, Leach.

#### 3. LEUCOTHOË SPINICARPA (*Abildgaard*).

*L. spinicarpa*, Chilton, 1912 (2), p. 478.

" " Barnard, 1916, p. 148.

*Localities.* Wooded Island, Easter Group, two specimens. Sandy Island, Wallaby Group, five specimens.

*Distribution.* Cosmopolitan.

*Remarks.* The two papers quoted above give the full synonymy of this species and full notes on its known distribution.

#### Family GAMMARIDÆ.

##### Genus CERADOCUS, A. Costa.

#### 4. CERADOCUS RUBROMACULATUS (*Stimpson*). (Pl. 1. figs. 15, 16.)

*C. rubromaculatus*, Stebbing, 1906, p. 430 (synonymy).

" " Walker, 1904, p. 272; 1905, p. 927; and 1909, p. 334.

" " Chevreux, 1907, p. 479.

" " Stebbing, 1908 (1), p. 81; 1908 (2), p. 456; 1910 (1), p. 598.

" " Chilton, 1916, p. 369.

*Locality.* Sandy Island, Wallaby Group, one female, 10 mm., and one male and two females, 6 mm.

*Distribution.* Ceylon, the Maldives and Laccadives, and the coast of Africa (Walker); South Africa (Stebbing); Australia and Tasmania (Haswell & Stebbing); New Zealand (Chilton); French Oceania (Chevreux).

*Remarks.* From the published descriptions and figures, this species would appear to be subject to great variation in the antennæ, antennules, first and second gnathopods, fifth peræopods, and in the size and extent of the serrations on the margins of the pleon and its epimeral plates.

These facts have led me to ascribe all the four specimens in this collection to the same species, notwithstanding the differences and the extraordinary dimorphism in the second gnathopods of the only male specimen.

In the large female specimen, 10 mm. in length, the dorsal surface of the pleon is microscopically shagreened. The teeth on the posterior margins of the first three segments are longer and coarser than in the smaller specimens, and there is a seta alternating with every tooth. The epimeral plate of the first pleon segment has two teeth on the lower border and eight on the hinder border, or ten teeth in all. The second pleon segment has five teeth on the margins of the epimeral plate, and the third segment fourteen teeth. It is not easy to decide where the lower and hinder margins meet. The antennal peduncle is equal in length to the antennular. The accessory flagellum of the antennule has seven joints and the main flagellum twenty-five. The flagellum of the antenna has fourteen joints. The hinder lower corner of the second joint of the fourth and fifth peræopods is prolonged into a spine, as figured by Chevreux (1907) for specimens from French Oceania.

In the smaller specimens the teeth on the dorsal border of the first three pleon segments are shorter and finer than in the larger specimen. The epimeral plates of the first two segments of the pleon have one or two teeth on the lower border but none on the hinder. The third segment of the pleon has six teeth on the hinder border and two on the lower border of the epimeral plate. The flagellum of the first antenna has seven joints and the accessory appendage four joints. The flagellum of the second antenna has from 15–21 joints. The hinder lower corner of the second joint of the fourth and fifth peræopods is much less produced than in the large specimen, and is more like the typical form.

The male specimen presents a striking dimorphism in the second gnathopods. The right one is of the normal type, the palm rather oblique and furnished with two flat-topped teeth. It is not so robust as in the specimens figured by Chevreux from French Oceania, and the palm is more oblique and not transverse. But Chilton describes specimens from New Zealand which appear to agree with mine. The second gnathopod on the left side is quite different. The propodus is larger and more robust, the palm very oblique with no prominent tooth marking its edge, but with a very strong obtuse



tooth near the base of the nail. The whole limb recalls to some extent that found among the males of the genus *Elasmopus*, though it is not setose at all. Stebbing, in the 'Challenger' Report and in recording this species from South Africa, notes the dissimilarity between the right and left second gnathopods in some of his specimens; but the dissimilarity usually takes the form of one of the gnathopods being of the female type and the other of the male. No such striking instance as the present one has been noticed before.

With regard to the serrations on the epimeral plates of the first three segments of the pleon, the typical form has one or two serrations on the lower margin in all three segments, but only the third segment is serrated on the hind margin. Chevreux describes serrations on both lower and hinder margins of the epimeral plates of the second and third pleon segments in specimens from French Oceania. Haswell says of Australian specimens "lateral plates (epimera) of the three anterior segments of the pleon serrated posteriorly," while in *Mæra spinosa*, now regarded as a synonym of *C. rubromaculata*, he gives only the third segment with serrations on the posterior margin of the lateral plate. There is thus abundant evidence of variation in this character. I may note that, in all my specimens, the first joint of the mandibular palp has a spiniform process on its inner corner as described by Walker (1904) and Chevreux (1907).

### Genus *MÆRA*, Leach.

#### 5. *MÆRA TENELLA* (Dana).

*Gammarus tenellus*, Dana, 1852, p. 952, pl. 65. fig. 7.

*Mæra tenella*, Walker, 1904, p. 272, pl. 5. fig. 31.

*M. tenella*, Stebbing, 1906, p. 438.

*Locality.* Wooded Island, Easter Group, one male, 5 mm.

*Remarks.* The single specimen agrees closely with the description and figures of a specimen from Ceylon referred to Dana's species by Walker. The only noteworthy point of difference is that the dactylus of the second gnathopods in the male has a well-marked tooth about the centre of its inner margin, which fits into a corresponding excavation on the palm. The serrate hind margin of the third segment of the pleon and the slightly different form of the second gnathopods of the male seem to distinguish this species from *M. viridis*, Haswell, to which it is otherwise very closely allied; in fact, this species seems to me to afford an additional argument in support of Chilton's contention that Haswell's species belongs to the genus *Mæra*, and not to *Elasmopus* to which Stebbing would refer it.

*Distribution.* Fiji (Dana); Ceylon (Walker).

6. *Mæra mastersii* (Haswell).

*Megamæra mastersii*, Haswell, 1880 (1), p. 205, pl. 11. fig. 1.

*M. thompsoni*, Miers, 1884, p. 318, pl. 34. fig. B.

*Mæra mastersii*, Stebbing, 1906, p. 439.

" " Chevreux, 1907, p. 481.

" " Stebbing, 1910 (1), p. 642.

" " Chilton, 1911, p. 564.

" " Barnard, 1916, p. 195.

" " Chilton, 1918, p. 367.

*Locality.* Sandy Island, Wallaby Group, one male, 5 mm.

*Distribution.* Port Jackson, Australia (Haswell); several localities in the Torres Strait (Miers); Gambier Archipelago (Chevreux); Kermadec Islands (Chilton); Mozambique (Barnard); New Zealand (Thomson & Chilton).

## Genus ELASMOPUS, A. Costa.

7. *ELASMOPUS SUBCARINATUS* (Haswell).

*Megamæra subcarinata*, Haswell, 1880 (2), p. 335, pl. 21. fig. 4.

*Elasmopus subcarinatus*, Chilton, 1915, p. 321, figs. 1-6.

*Locality.* Dredged off Wallaby Group, one male, 6 mm.

*Distribution.* Shores of New Zealand, Australia, Ceylon, South Africa, and Indian Ocean.

*Remarks.* Chilton, in the paper quoted above, has given a full account and synonymy of this species and of its geographical distribution. The species is distinguished from its congeners by the two carinæ of the fourth segment of the pleon each ending in a prominent tooth. In this character my specimen agrees with the type, but it differs from typical specimens as described by Chilton in the following characters:—

- (1) In the first antennæ, which are much shorter than usual and have only fifteen joints in the flagellum. The accessory appendage is quite short and only has two joints. Walker recorded specimens from Ceylon in which the accessory appendage of the first antenna was only two-jointed.
- (2) In the hinder margin of the second joint of the last pair of peræopods, which is closely and coarsely pectinate as described for the species *E. pecteniscrus*, Sp. Bate. Chilton says of all the peræopods that the "basal joint . . . . . posterior margin simply serrate," while Stebbing says that the margins are "strongly serrate." But the condition in the present specimen agrees with Walker's description in *E. serrula* (= *E. pecteniscrus*): "the greater part of the hind margin elegantly cut into flat-topped

teeth of a peculiar form" (Walker, 1904). Barnard (1916), in describing *E. pecteniscrus*, Bate, from S. Africa, to which species he refers Walker's *E. serrula* as a synonym, figures the second joint of the fourth peræopod, showing a condition exactly similar to the second joint of the fifth peræopod in my specimen. I may note that on one side the hinder margin of the second joint of the fifth peræopod is concave and on the other convex or evenly curved. Barnard suggests that the concave margin is a condition of maturity. The fifth peræopods of my specimen are not so setose as is described by Chilton for New Zealand specimens. Having only one specimen, it is impossible to say whether these differences are constant and of specific value. The two dorsal curinæ of the fourth pleon segment exclude this specimen from all other described species, and in the character of the second gnathopods the specimen is a typical adult male of *E. subcarinata* as figured by Chilton. I prefer, therefore, to regard the specimen as at most an individual variation of this widely distributed species.

#### Family PHOTIDÆ.

##### Genus EURYSTHEUS, Bate.

#### 8. EURYSTHEUS ATLANTICUS (Stebbing). (Pl. 1. figs. 17-20.)

*Gammaropsis atlantica*, Stebbing, 1888, p. 1101, pl. 114.

*G. zeylanicus*, Walker, 1904, p. 282, pl. 6. fig. 41.

*G. gardineri*, Walker, 1905, p. 929, pl. 88. figs. 11-14, 16-17.

*Eurystheus atlanticus*, Stebbing, 1906, p. 611.

*E. atlanticus*, Stebbing, 1908, p. 86 (1), pl. 40 B.

*E. zeylanicus*, Walker, 1909, p. 339.

*E. atlanticus*, Walker, 1909, p. 339.

" " Stebbing, 1910 (1), p. 614.

**Locality.** Dredged off Wallaby Group, one female with ova, 6 mm.; one adult male, 6 mm.; two young males, 4 and 4.5 mm.

**Distribution.** Cape Verde Islands (Stebbing), Ceylon, Maldives and Laccadive Archipelagoes, Seychelles (Walker), S. Africa (Stebbing), Australian coasts (Stebbing).

**Remarks.** These four specimens are all imperfect; only one, the larger of the immature males, has any of the antennæ still attached, and that only the peduncle with the accessory appendage on one side only. The accessory appendage is composed of four joints, three large ones and a small terminal one.

Only the two larger specimens have the lageniform eyes characteristic of the species. In the two smaller specimens the neck of the flask, so to speak, is wanting.

I have figured the distal joints of the second gnathopods of all four specimens. The second gnathopods of the female agree very fairly well with those figured for *E. afer* by Stebbing (1888), for *E. zeylanicus* by Walker (1904), and for *E. gardineri* by Walker (1905). Those of the smaller immature male resemble the figures given by Stebbing for the type-specimen (a female) from Cape Verde (1888, pl. 114, gn. 2) of *E. atlanticus*, by Walker for the young male of *E. zeylanicus* (1904, pl. 6, fig. 41, gn. 2, ♂ jr.), and by Walker for the young male of *E. gardineri* (1905, pl. 88, fig. 14).

The second gnathopods of the larger of the immature males agree closely with those figured for the adult male of *E. zeylanicus* by Walker (1904, pl. 6, fig. 41, gn. 2, ♂), and is not unlike the figures given by Stebbing for the adult male of *E. atlanticus* (1908 (1), pl. 40 B). Stebbing's specimen had, however, lageniform eyes.

The second gnathopods of the adult male are not quite like those figured for any of the species of *Eurystheus*, but seem to be the adult condition of the immature males in this collection. I feel convinced that the four specimens here dealt with belong to one species. They were all collected at the same time in the same place, and appear to me to represent the adult female and three stages of growth in the male. From this it follows that the lageniform shape of the eyes is an adult character only, or, alternatively, a character which varies greatly. I feel sure, too, that my specimens belong to the same species as *E. zeylanicus*, Walker, and *E. gardineri*, Walker. Neither of these species has lageniform eyes, but judging from my specimens, most of Walker's specimens were immature. Walker himself in 1909 united these two species, and in a footnote to the same paper expresses the opinion that both are synonymous with *E. atlanticus*, Stebbing. In accepting that verdict, it is necessary to point out that the type of *E. atlanticus* is a female which has the lageniform eyes of the adult and second gnathopods of the form ascribed here to an immature male with oval eyes. Both (Chilton 1912 (2) and Barnard (1916) have suggested the possibility of *E. atlanticus* being the same as *E. afer* (Stebbing), and support is given to that idea by the close resemblance of the second gnathopods of the adult female in the present collection to those figured by Stebbing for *E. afer*, female. But the latter species has long oval eyes, not lageniform in shape. Chilton's specimens, identified with doubt as *E. afer*, seem to have gnathopods altogether longer and more slender than in the present specimens.

It will be seen that there has been considerable difficulty in arriving at a conclusion with regard to the identity of these specimens. I can best sum up the evidence yielded by them, by saying that they are certainly the same as *E. zeylanicus* and *E. gardineri* of Walker, and that I accept his opinion that these species are synonymous with *E. atlanticus*, Stebbing, a widely distributed and apparently very variable species.

## Family AMPHITHOIDÆ.

Genus GRUBIA, *Czerniavsky*.9. GRUBIA SETOSA (*Haswell*). (Pl. 2. figs. 21-24.)*Amphithoë setosa*, Haswell, 1880 (1), p. 270.*Grubia setosa*, Stebbing, 1906, p. 644.

*Localities.* Four males and four females, up to 15 mm. in length, from Sandy Island, Wooded Island, and Pigeon Island. (Shore collecting in each case.)

*Distribution.* Sidney Harbour and Botany Bay, New South Wales (Haswell & Chilton).

*Remarks.* Haswell's original description is short and unaccompanied by figures, but the present specimens are in agreement with it. Chilton, who examined specimens from Sydney Harbour which he referred to this species, stated that the first antenna possessed a small accessory appendage. The present specimens, or at least such of them as still retain the first antenna, possess a small two-jointed accessory flagellum on that appendage, barely longer than the first joint of the main flagellum. The species is therefore a true *Grubia*, in which genus Stebbing has already placed it.

The species is mainly distinguished by the form of the first and second gnathopods in both sexes, and especially by those of the male. I figure these appendages herewith. They are similar in the male and female, but in the former they are more massive and are densely fringed with long, delicate, plumose setæ, especially on the second, carpal, and propodal joints. The palmar margin is undefined in the first gnathopod, but in the second it is bounded by a rather prominent tooth, on the inside margin of which is a strong spine. In the second gnathopod of the male the limiting tooth is stronger, and immediately inside it on the palm is a small excavation into which the nail fits. The nail in both gnathopods is provided with a closely-set row of blunt spines on the inside margin. The figures will serve to show the general form of these limbs and the proportions of the joints.

For the rest, the species has no very marked characters. The first antennæ are almost as long as the whole animal, the third joint of the peduncle about  $\frac{1}{2}$  as long as the second, and the flagellum composed of about 50 joints. The second antennæ are  $\frac{2}{3}$  as long as the first. The fourth joint of the peduncle reaches to the distal end of the second joint of the peduncle of the first antennæ. The fifth joint equals the fourth in length, and the flagellum has 35 joints. The lower margin of the peduncle is beset with long plumose hairs, particularly in the male. The inner lobe of the first maxilla bears six or seven fine plumose setæ. The third uropods have the peduncle much larger than the rami, with a row of seven short, blunt spines on the dorsal apical margin. The inner ramus bears one spine and a number of setæ

at its apex. The outer ramus bears two recurved hooks of equal size and a short, blunt spine near the proximal end of the dorsal surface. In the light of Chevreux's description of *G. brevidactyla* and of the present species, Stebbing's diagnosis of the genus *Grubia* in 'Das Tierreich' will require emendation in the following points:—antenna 1 has a short accessory flagellum of one or two joints, and maxilla 1 the inner plate with a few small lateral setæ.

The present species is distinguished by the form of the first and second legs and, possibly also, by the structure of the third uropods.

## ISOPODA.

### Tribe FLABELLIFERA.

### Family SPHÆROMIDÆ.

### Group HEMIBRANCHIATA.

### Genus CILICÆOPSIS, *Hansen*.

*CILICÆOPSIS DAKINI*, sp. n. (Pl. 2. figs. 25–29; Pl. 3. fig. 34.)

*Locality.* Woody Island, Easter Group, one adult male, 13 mm. long, 9 mm. broad.

*Description.* The single specimen of this new species, a male, measures 13 mm. in length and 9 mm. in breadth, and is thus one and a half times as long as broad. The body is strongly convex in dorsal view and without granulations or tubercles. The posterior margins of all the thoracic somites, the lateral margins of the body, the uropods, and the abdomen are fringed with short, thick hairs, the general appearance of which can be seen from Pl. 3. fig. 34. Similar hairs are scattered over the dorsal surface of the abdomen, especially on the two large bosses. The distinguishing features of the species are to be found in the abdomen and uropods. The abdomen shows three proximal segments separated off from the large terminal telsonic somite: the sutures separating the first two abdominal somites not complete in the mid-dorsal line. The posterior margin of the third abdominal somite is considerably and broadly produced in the mid-dorsal line, but does not form a process of any kind. The terminal abdominal somite bears two relatively enormous mammiform bosses. The posterior margin is evenly rounded, and shows the merest trace of a median process separated by shallow notches from the rest of the margin. The uropods consist of a massive basal joint and a long, narrow, terminal joint. The basal joint, I take it, represents the fused basipodite and endopodite, and the long terminal joint the exopod.

The figures which I give of the epistome, the antennule, antenna, second and eighth thoracic limbs will suffice to show the general features of these

appendages. The epistome is quite truncate anteriorly; the front margin fringed with short, thick hairs similar to those on the rest of the body. The second to the eighth thoracic limbs are bi-unguiculate and characterised by the development of strong spines on the inner margins of the merus, carpus, and propodus.

The pleopods are of the typical hemibranchiate type. The exopod of the third, fourth, and fifth pairs is two-jointed. In the third pair the margins of the endopod and the distal joint of the exopod are fringed with plumose setæ. In the fourth and fifth pairs there are no plumose setæ, but the outer margins of both branches of the fifth pleopods possess a fringe of simple short hairs. The appendix masculina on the second pleopods is longer than the branches, with the terminal portion narrower than the rest and slightly hooked.

This species differs from the definition of the genus *Cilicreopsis* given by Hansen (1905) in possessing a vestige of a mesial lobe on the posterior margin of the last abdominal somite, and from the type-species *C. granulata* (Whitelegge) and its ally, *C. whiteleggei* (Stebbing), in being without a long process from the median portion of the anterior part of the abdomen. In this latter character it agrees, however, with *Cilicra stylijera*, Whitelegge, and *C. ornata*, Whitelegge, which Hansen refers tentatively to the genus *Cilicreopsis*. It may be noted that both the last-named species show a further resemblance to *C. dukini* in having the posterior margin of the third abdominal somite produced in the mid-dorsal line.

I know of no species of the group Cymodocini with which the present species can be confused in the form and structure of the abdomen, and I have pleasure in associating it with the name of its discoverer.

#### Genus *Cymodoce*, Leach.

##### *Cymodoce mammifera*, Haswell (?). (Pl. 3. fig. 35.)

*C. mammifera*, Haswell, 1880 (4), p. 474, pl. 18. fig. 1, 1 r.

*Locality.* Off Wallaby Islands, dredging, two specimens, 12 mm.

*Remarks.* It is with some doubt that I refer these two specimens to Haswell's species, but they agree completely with his short description and figures. Of the two specimens, one is apparently an immature male in so far as it has a pair of penial filaments on the sternum of the last thoracic somite, but no appendix masculina on the second pleopods. The other is a female. The species is a typical hemibranchiate sphaeromid in the structure of the pleopods, and would seem to fall into the genus *Cymodoce* by the well-developed mesial lobe in the abdominal notch, by the absence of a mesial process on the abdomen of the male, and by the well-developed endopod of

the uropods. The body in both sexes is smooth, except for a sparse coating of short fine hairs on the sides of the thorax and on the abdomen and the uropods. There are no granulations or small tubercles. In the male, the abdomen of which I have figured, the posterior margin of the fourth abdominal somite, which is completely separated from the terminal part of the abdomen, is produced into two small tubercles, one on each side of the middle line. The terminal part of the abdomen has two large mammiform bosses on the dorsal surface separated by a shallow depression, each with a small tubercle on the highest part of the boss. The posterior margin of the abdomen is tridentate, a large mesial lobe separated by notches from a small lateral lobe on each side. The large median lobe is very much bigger than the lateral lobes and almost masks them in dorsal view. The uropods are shorter than the median lobe of the abdominal notch, the endopod well-developed and as long as the exopod, with the apex truncate; the apex of the exopod is rather acute. The female differs from the male in being without the tubercles on the posterior margin of the fourth abdominal somite, and in having the bosses on the terminal portion of the abdomen less well-marked than in the male and without the tubercle on their highest parts.

Haswell's types were collected at Port Denison in Queensland, and the species does not appear to have been met with since. The species was omitted from Haswell's 'Catalogue of Australian Crustacea,' and has been lost sight of since the original description appeared in 1880.

*CYMODICE PELSARTI*, sp. n. (Pl. 2. figs. 30-33; Pl. 3. fig. 36.)

*Localities.* Sandy Island, two males, 9-12 mm. Pigeon Island, one male, 8 mm.; one female, 6 mm.; and six juv.

*Description of the Male.* The sides of the thoracic somites and the whole of the abdomen and uropods are fringed with rather long hairs. Similar but much shorter hairs are sparsely scattered over the dorsal surface of the thorax. The thoracic somites have a double row of small round tubercles extending as a band right across the posterior portion. These tubercles are rather obscure on the anterior somites, but become successively more clearly marked on the posterior ones. They are more clearly defined in the larger specimens. The abdomen has an ornamentation of granules and tubercles, as shown in Pl. 3. fig. 36, which is taken from a male specimen, 9 mm. in length. The whole of the abdomen and dorsal surface of the uropods is finely granulose, and scattered among the small granulations are larger rounded tubercles and a few still larger and pointed tubercles. The posterior margin of the fourth abdominal somite, which is complete right across the dorsal surface, is produced into two prominent pointed tubercles, one on each side of the middle line. Each of these tubercles bears a clump of long hairs immediately in front. The remainder of the anterior portion of the abdomen



is covered with larger and smaller tubercles. The posterior part of the abdomen has, in the main, three large bosses—an anterior pair, one on each side of the middle line, and behind them a single median posterior boss. The anterior pair of bosses are somewhat elliptical in shape, and each bears a large, prominent, almost erect, conical spine with additional spines at its apex. Behind this prominent spine are four or five sharply-pointed tubercles, more prominent than the rest of the tubercles and granulations covering the surface. The posterior median boss is circular in outline, quite smooth and polished, and bearing a single almost erect stout conical spine. The posterior margin of the abdomen is tridentate; the median lobe rather longer than the lateral lobes, with the apex truncate and bearing two spine-like tubercles. The lateral lobes have their apex pointed and bearing a single spine-like tubercle. The uropods extend some way behind the posterior margin of the abdomen; their dorsal surface is covered with fine granulations, with here and there a larger and more prominent tubercle. The inner branch is longer and stouter than the outer; its apex obtusely rounded, with a spine-like tubercle at its tip. The outer branch is more pointed than the inner, and has a similar spiniform tubercle at the apex. The mouth-parts and thoracic appendages present no special features, and the figures which I give of the peduncles of the antennules and antennæ, second and eighth thoracic limbs will serve to show the general structure of these appendages. The second to the eighth thoracic limbs are stout and bi-unguiculate, with an armature of strong spines on the inner margin of the merus, carpus, and propodus.

The pleopods are typically hemibranchiate, with the exopods of the third, fourth, and fifth pairs two-jointed. The appendix masculina on the second pair of the male is nearly twice as long as the branches, narrowing to a finely-pointed apex, the distal portion curved slightly inwards.

The female differs from the male in having the body smooth, without tubercles and granules, and with the hairs on the thorax and abdomen very short and very much less numerous. The anterior part of the abdomen, *i.e.* the combined first four segments, has the general surface raised into two obscure bosses. The terminal portion of the abdomen has likewise two bosses, more clearly defined and separated medianly by a shallow groove. The posterior margin is tridentate; the median lobe somewhat larger than the lateral lobes, with its apex bluntly rounded.

Among all the described species of the genus *Cymodoce*, this species comes nearest to *C. pilosa*, M. Ed., and its allies *C. longistylis*, Miers, *C. bicarinata*, Stebbing, and *C. canzibarensis*, Stebbing, but differs from all of these species by the large, conical, erect spine which crowns each of the three main bosses of the abdomen. I have associated the name of the discoverer of the Abrolhos group of islands with this pretty little species found there by Professor Dakin.

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## EXPLANATION OF THE PLATES.

## PLATE 1.

*Parawaldeckia kidderi* (S. I. Smith).

- Fig. 1. Telson,  $\times 680$ .  
 2. Peduncle of antenna of male,  $\times 33$ .  
 3. Second thoracic leg,  $\times 33$ .  
 4. Third " "  $\times 33$ .  
 5. Fifth " "  $\times 33$ .  
 6. Eighth " "  $\times 33$ .

*Parharpinia villosa* (Haswell).

- Fig. 7. Mandible,  $\times 57$ .  
 8. Maxilliped,  $\times 57$ .  
 9. Second thoracic leg,  $\times 33$ .  
 10. Third " "  $\times 33$ .  
 11. Fifth " "  $\times 33$ .  
 12. Sixth " "  $\times 33$ .  
 13. Seventh " "  $\times 18$ .  
 14. Eighth " "  $\times 33$ .

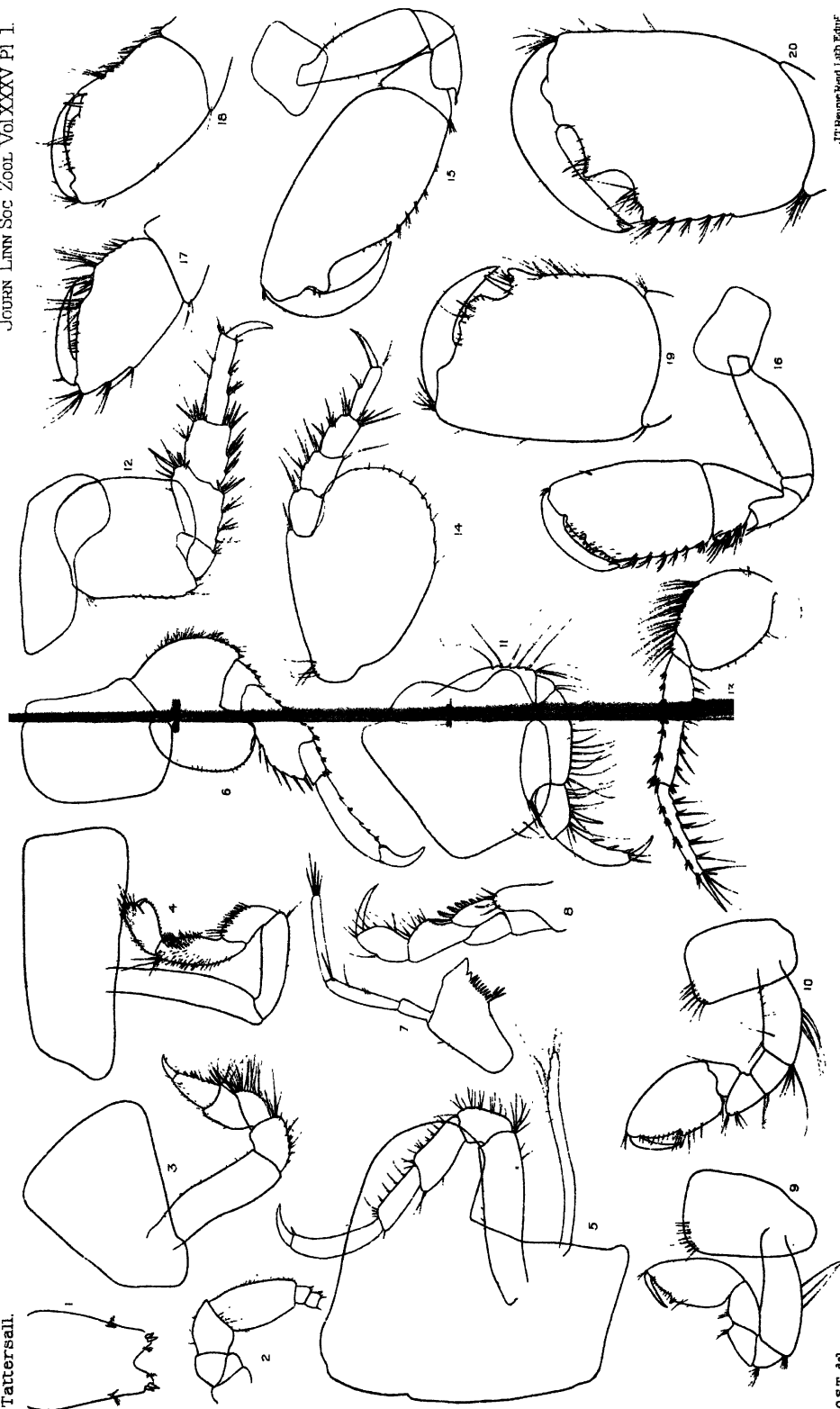
*Ceradocus rubromaculatus* (Stimpson).

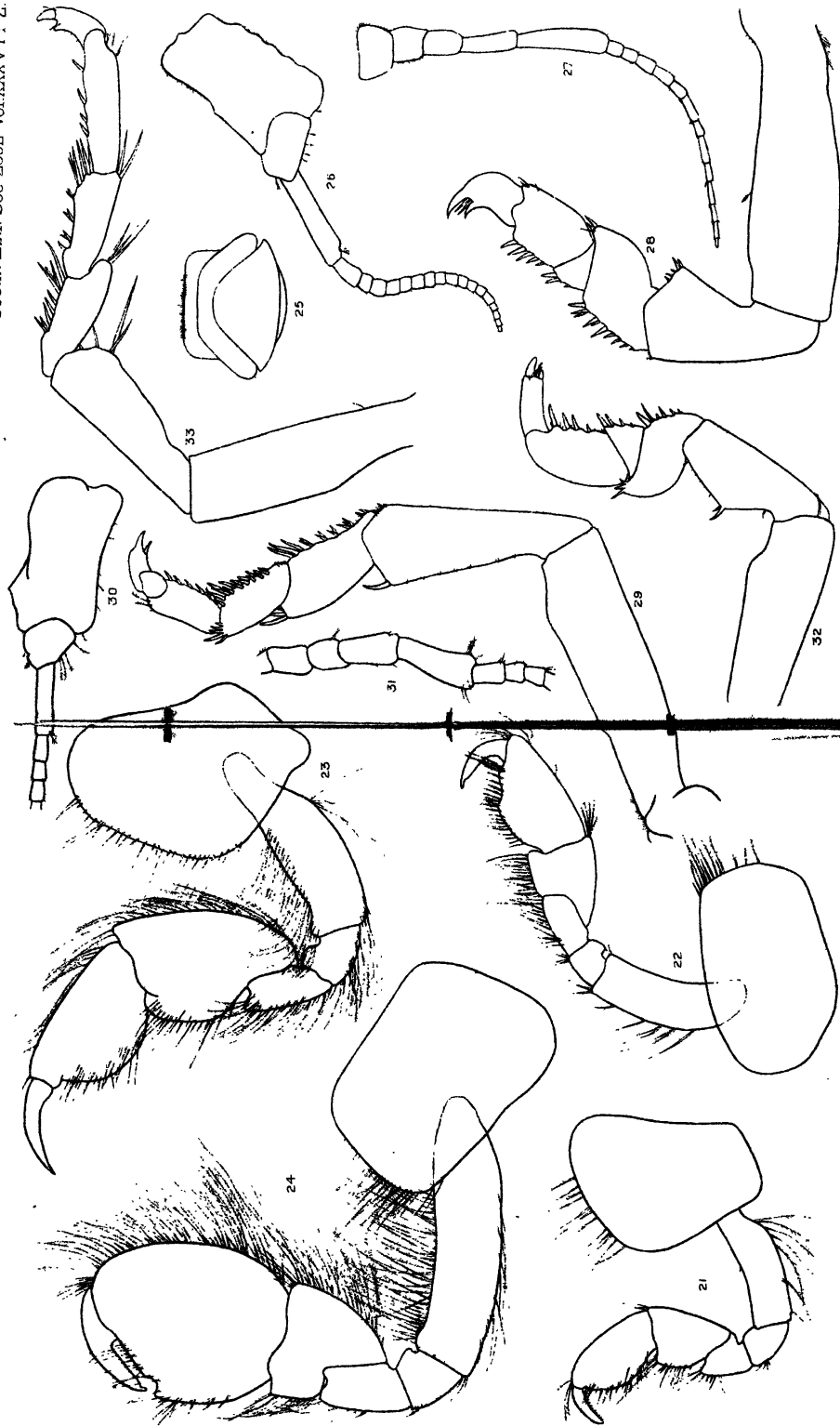
- Fig. 15. Left third thoracic leg of male, 6 mm.,  $\times 33$ .  
 16. Right " " " same specimen,  $\times 33$ .

*Eurystheus atlanticus* (Stebbing).

- Fig. 17. Hand of third thoracic limb of female with lageniform eye,  $\times 460$ .  
 18. Hand of third thoracic limb of young male with oval eye,  $\times 460$ .  
 19. Hand of third thoracic limb of young male with oval eye,  $\times 460$ .  
 20. Hand of third thoracic limb of adult male with lageniform eye,  $\times 460$ .



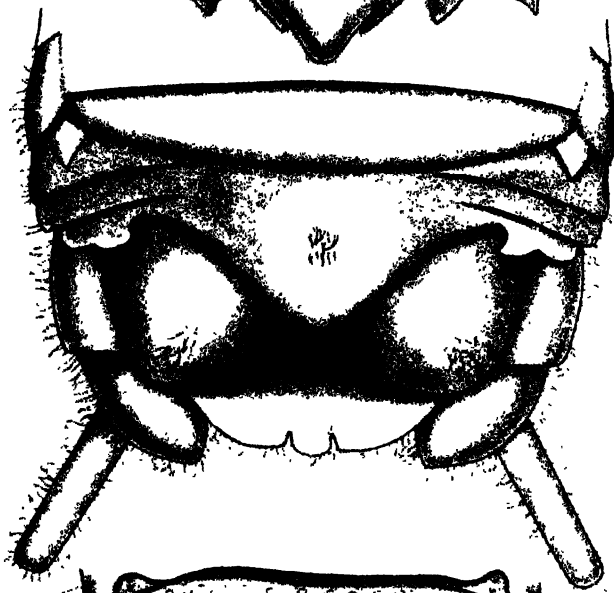




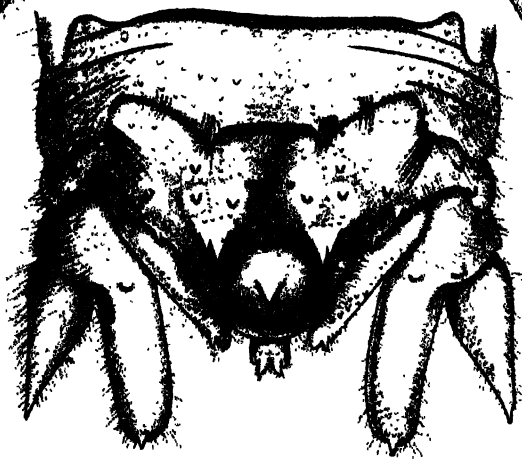




35



34



36

O & T del.

J. T. Remme Rand Lith. Edinb.





## PLATE 2.

*Grubia setosa* (Haswell).

- Fig. 21. Second thoracic limb of female,  $\times 22$ .  
 22. Third       "       "       "        $\times 22$ .  
 23. Second     "       "       male,  $\times 22$ .  
 24. Third       "       "       "        $\times 22$ .

*Ciliceopsis dakini*, sp. n.

- Fig. 25. Epistome.  
 26. Antennule of male,  $\times 22$ .  
 27. Antenna     "       "        $\times 22$ .  
 28. Second thoracic limb,  $\times 22$ .  
 29. Eighth     "       "        $\times 22$ .

*Cymodoce pelsarti*, sp. n.

- Fig. 30. Antennule of male,  $\times 33$ .  
 31. Antenna     "       "        $\times 33$ .  
 32. Third thoracic limb,  $\times 33$ .  
 33. Eighth     "       "        $\times 33$ .

## PLATE 3.

- Fig. 34. *Ciliceopsis dakini*, sp. n., abdomen of male,  $\times 10$ .  
 35. *Cymodoce mammifera*, Haswell, abdomen of young male,  $\times 11$ .  
 36. *Cymodoce pelsarti*, sp. n., abdomen of male,  $\times 16$ .

[I am greatly indebted to my wife for the drawings illustrating  
 this report.]



THE PERCY SLADEN TRUST EXPEDITIONS \* TO THE ABROLHOS  
ISLANDS (INDIAN OCEAN).

Under the Leadership of Prof. W. J. DAKIN, F.L.S, F.Z.S.

On Two Sea-pens from West Australia. By SYDNEY J. HICKSON, F.R.S.,  
Professor of Zoology, University of Manchester. (Communicated by  
Prof. W. J. DAKIN, F.L.S.)

[Read 5th May, 1921.]

At the present time only three species of Pennatulacea have been recorded from the waters of the Western coast of Australia, and these were all found in Shark's Bay, over 200 miles north of the locality from which the two species here recorded were obtained. The species previously recorded are *Policella australis* by Gray (1862), *Virgularia elegans* by Gray (1870), and *Pteroides hymenocaulon* by Broch (1910).

The two specimens obtained by Professor Dakin from the neighbourhood of the Abrolhos Archipelago belong to, or are closely related to, species that are found in the Malay Archipelago; but as other species of the same genera, namely *Veretillum cynomorium* and *Pteroeides griseum*, occur in the Mediterranean Sea, and the genera are widely distributed in shallow to deep water, the presence of the two sea-pens off Abrolhos is a fact of no value, at present, for the determination of the affinities of the local fauna. It is quite possible, or even probable, that they have travelled down from the North, but it would not be surprising to find them a great deal further South, as they are not tropical forms.

VERETILLUM MALAYENSE (*Hickson*) †. 20 fathoms. Off Long Island.

Length of rachis 80 mm., length of stalk 60 mm., diameter of rachis and of stalk 12 mm., diameter of terminal bulb 14 mm. Autozooids 14 mm. in length by 2.5 in diameter.

The rachis is club-shaped, but differs from the rachis of the type-specimen in coming gradually to a blunt extremity. The stalk has a well-marked

\* Acknowledgement must be made here also of a grant from the Government Grant Committee of the Royal Society, and a grant from the British Association.

† 'Siboga' Pennatulacea, 1916, p. 48.

basal bulbous swelling. The autozooids are large, and most of them are fully expanded. The siphonozooids are numerous and irregularly scattered on the rachis; they extend a considerable distance down the stalk beyond the last autozooid. The stomodæa have a dorsal ventral diameter of 0.14 mm. The axis is well developed, quadrangular in section, the diagonal measurement being 1.5 mm. in its thickest part. I have not dissected out the axis from this beautifully preserved specimen, but it can be seen through the transparent tissues to be at least two-thirds of the total length of the colony.

The spicules of the rachis are long, thin plates with jagged edges, large ones measuring  $0.25 \times 0.07$  mm., but they are very variable in shape and size, and scattered or clustered. In the expanded part of the autozooids, spicules are very scarce. I have seen one or two at the base of the tentacles, but none in the tentacles themselves.

The type-specimens of this species were found in the Bay of Bima on Sumbawa Island, Malay Archipelago, at a depth of 55 metres, and I have been able to compare the characters of the specimen from W. Australia with the type-specimens which are at present under my care. The specimens from Shark's Bay that were named by Gray *Policella australis* were transferred to the genus *Veretillum* by Kükenthal and Broch, and, in my opinion, this transference was fully justified.

The principal difference between the species *Veretillum malayense* and *V. australe* is that the autozooids of the former are about twice the size of the autozooids of the latter. This character—the size of the autozooids—may be more variable than we are justified in assuming on our knowledge of the half-dozen specimens that have been described, and the two species may be merged into one in the near future. But it is clear that the specimen described above agrees more closely with the specimens hitherto called *V. malayense* than it does with those described as *Policella* (or *Veretillum australis*).

PTEROIDES sp. ?, juv. 20 fathoms. Outside Wallaby Group.

Length of rachis 25 mm., length of stalk 31 mm. Leaves 11–10. Number of rays on largest leaves 5. Siphonozooid plate basal.

This specimen is evidently a juvenile form, as is shown by its small size, by the small number of leaves, by the rudimentary character of the lower leaves, and by the relative length of the stalk. It may also be regarded as a sign of juvenility that there is only a single row of autozooids on the greater part of the margin of the largest leaves, an additional autozooid of what may be a second row appearing only in one or two isolated places.

As it is impossible, in the present state of our knowledge, to determine accurately the relations of the juvenile forms of this genus, the principal point of interest is to consider whether it is a juvenile of the only species of

the genus that has hitherto been identified from the West coast of Australia, namely *Pt. hymenocaulon*. Broch (1910) examined and carefully described two specimens of this species from Shark's Bay. One was 94 mm. in length and one 140 mm. in length, and therefore it is probable that they possessed most of the adult characters. My reasons for believing that the young specimen from the Wallaby Group is not *P. hymenocaulon* are: (1) that the siphonozoid plate is marginal in *P. hymenocaulon* and basal in our specimen, and (2) that the spicules in the stalk of *P. hymenocaulon* are smaller and more numerous than in our specimen. I do not wish to maintain that these reasons are conclusive, but I am inclined to think that the species to which the specimen belongs is one of my Group II. 3 (see Monograph on 'Siboga' Pennatulacea, p. 231), represented by such species as *Pt. griseum* or *Pt. malayense*.



The Raninidæ: a Study in Carcinology. By GILBERT C. BOURNE, M.A., D.Sc., F.R.S., F.L.S., late Fellow of Merton College, Oxford, and Linacre Professor of Zoology and Comparative Anatomy.

(PLATES 4-7.)

[Read 15th December, 1921.]

MM. A. MILNE EDWARDS and E. L. BOUVIER conclude the Introduction to their Report on the Deomiacea and Oxystomata dredged by the U.S. Coast Survey Steamer 'Blake' with the following sentence:—"Nous avons distrait du groupe des Oxystomes la famille des Raninidés qui nous paraît aberrante à plus d'un titre. Ces Oxystomes anormaux sont représentés par de curieuses formes nouvelles dans les matériaux recueillis par le Blake; nous les étudions avec la plus grand détail, et ils font prochainement l'objet d'une étude très complète." So far as I have been able to ascertain by search in the records of zoological literature, somewhat incomplete as they are through disturbances arising out of the late war, this promised memoir on the Raninidæ has not yet been published, and the following pages give an account of my own studies on this aberrant and, as I shall strive to show, primitive family of crabs. My attention was directed to them some eight years ago, and I spent some time in the attempt to procure a well-preserved specimen of *Ranina*, of which I had several ill-preserved examples collected by Messrs. C. & E. Hose in Celebes. Eventually, after much fruitless correspondence with other naturalists, I obtained a fine specimen of *Ranina dentata* from Professor Kishinoye, of Tokio. It was admirably preserved in spirit, and I have to express my best thanks to him for his trouble in procuring me so excellent an example for study and dissection.

In addition to *Ranina*, I had examples of the following members of the family in the collections of the Oxford University Museum:—

*Notopus dorsipes*, Fabr.; two examples collected by H.M.S. 'Nassau' in the Sulu Sea, 1871-72.

*Raninoides personatus*, White MS., Henderson; one example from the Bay of Bengal, presented to the University by the Calcutta Museum.

*Lyreidus tridentatus*, de Haan; two examples from Port Jackson, presented to the University by the Trustees of the British Museum of Natural History.

Two examples of a species labelled "Notopus," collected in the Sulu Sea by H.M.S. 'Nassau.' These I am describing as a new genus and species under the name of *Notosceles chimmonis*.



I have also been able to examine the following species in the British Museum of Natural History, and take this opportunity of thanking Dr. W. T. Calman for his courtesy and assistance in bringing the material together for examination :—

*Notopoides latus*, Henderson.

*Notopus ovalis*, Henderson.

*Lyreidus Channeri*, Wood-Mason.

*Zanclifer caribensis*, de Freminville.

*Cosmonotus Grayi*, Adams & White.

The above are preserved in spirit. I also had the opportunity of examining a dried specimen labelled *Ranilia muricata*, M. Edw., and am inclined to the opinion that, while it is a distinct species, it is closely allied to and should be placed in the genus *Notopus* of de Haan.

Thus I have had opportunities of studying more or less closely nearly all the known genera and most of the known species of the Raninidæ, which must be accounted one of the most ancient crab families, for it occurs in the Cretaceous along with other forerunners of existing crabs. The proper place of the Raninidæ in classification has always been a subject of dispute. Latreille first placed them among the Brachyura, but subsequently removed them to the Macrura. Milne Edwards in his 'Histoire Naturelle des Crustacés' (25, 1837) includes them along with the Dromididæ, Homolidæ, and Pactolidæ as a tribe of his section Anomura Apterura. De Haan (34, 1850) showed that the resemblances between the Raninidæ and Hippidæ were superficial, and placed the former among the Oxystomata, laying special stress on the affinities of *Lyreidus* to the Leucosiidæ. "Uti in ceteris Oxystomatibus, os Raninoideorum parte anteriore est canaliculatum. Raninoidea et Leucosidea unicæ sunt formæ inter Decapoda, quorum regiones pterygostomianæ cum sterno cohærent, ita ut maxillarum quintarum articuli primi infra pulpos sint dispositi et radices ipsis regionibus pterygostomianis tegantur; unicæ, quorum cavitates branchiales a parte anteriore simplicem tantum aperturam offerunt, uti jam Cl. Edwards observavit. *Lyreidus* tam distinctum vinculum constituit inter *Raninas* et *Leucosias*, ut vix dubium remanere possit, quin justus hic sit illius familiæ locus."

Boas (4, 1885) retained the Raninidæ among the Brachyura, but laid stress on their abnormal characters, and concluded by saying, "il m'est impossible de comprendre . . . . pourquoi les Ranines sont rangées avec les autres Oxystomes." In the 'Challenger' Reports, Henderson (35, 1888), following Milne Edwards' arrangement, describes the Raninidæ among the Anomura, and the same author, in a subsequent memoir (36, 1893), makes them into a group, Ranidea, equivalent to his groups Dromidea and Hippidea of the Anomura. Ortmann (41, 1892) follows de Haan in placing the Raninidæ in the Oxystomata, and subsequently (42, 1901) erected the

Oxystomata into a division (Abtheilung) equal in value to the Dromiidea (Boas's Dromiacea) and the Brachyura, the last-named division including all other true crabs. This arrangement, with some minor modifications, has been adopted by Alcock (1, 1896), Borrodaile (12, 1904), and Calman (23, 1909). Against these authorities must be set the opinion of A. Milne Edwards and Bouvier, quoted above, and the similar judgment of Boas that the Raninidæ cannot be included in the Oxystomata. But if carcinologists differ as to the exact position that the Raninidæ should occupy among the crabs, it is now generally agreed (except Ortmann [42], who keeps the Oxystomata apart from the Brachyura) that they are true crabs belonging to the section Brachyura and not to the section Anomura of the Decapoda reptantia. Indeed, this was clearly established by de Haan seventy years ago, and it will be convenient to enumerate here the Brachyuran characters of the Raninidæ, most of which were recognised by the clear-sighted author of the volume 'Crustacea' of the 'Fauna Japonica.' They are :—(1) The reduced abdomen and the absence of uropods. (2) The absence of pleopods on the first abdominal somite of the female. (3) The absence of posterior abdominal appendages in the male. (4) The union of the pterygostomial region of the carapace with the epistome. (5) The adherence of the branchiostegite to the thoracic epimera. (6) The reduction of the branchiæ. (7) The absence of an exopoditic scale on the second antenna. (8) The presence of a sellae turcica posterior. (9) The expansion of the ischium and merus of the third maxillipeds to form a plate-like covering to the other mouth-parts. (10) The presence of orbits in which the eye-stalks can be concealed, and correlated with this the reduction in size of the first and second antennæ. Other characters might be mentioned, such as the specialisation of the thoracic limbs as organs of locomotion, involving a great development of the apodemes forming the walls of the cavities in which the muscles of the limbs are contained. In other words, it is part of the distinctive facies of a crab that the musculature is highly developed in connection with the locomotory thoracic limbs, and is feeble almost to the point of disappearance in the abdomen. This feature is strongly marked in the Raninidæ.

On the other hand, it is generally recognised that the Raninidæ exhibit a number of Macruran characters which, on the assumption that the Brachyura are descended from the Macrura, are primitive. Among the more important of these are :—The comparatively well-developed rostrum, which, however, is absent in *Cosmonotus*. The proximal segments of the second antenna are not fused with the epistome, a primitive feature also shared by the Dromiacea. The presence of a sternal canal and the relatively well-developed anterior thoracic apodemes. The narrow and keel-like posterior thoracic sternites. The oviducal apertures opening on the coxæ of the third pereopods, another primitive character shared with the Dromiacea. The external lobes of the

second maxillæ are narrow, the inner lobes normal (Ortmann). Finally, as I shall show, the nervous system is more Astacuran in type than in any other Brachyura. In addition, the Raninidæ exhibit a number of features peculiar to themselves, and these I shall discuss in detail in the later part of this paper.

For the present it is only necessary to refer to the theory originally propounded by Huxley and brilliantly sustained by Bouvier in his essay, 'Sur l'origine homarienne des Crabes' (22), that the crabs are not descended from Paguridæ nor from Galatheidæ nor Thalassinidæ, but directly from the Astacura, and in particular from the Homaridæ through the Dromiacea. "Les Dromiacés par l'intermédiaire des Homolodromies ou de formes très voisines, dérivent directement des Homaridés jurassiques ou de Homaridés qui leur ressemblent." Exception being made of such crab-like forms as *Porcellana*, *Lithodes*, and the *Porcellanopagurus* recently described by Borrodaile, Bouvier's theory of the origin of crabs is now generally accepted, and it follows that, if the Raninidæ be true crabs, they must be descended from a Homarid or Nephropsid ancestor by way of the Dromiacea. Thus Bouvier (22) has given convincing arguments for the derivation of the Dorippidæ from the Dromiacea, and Alcock (2) sees in his genus *Cymonomops*, which differs but little from *Cyclodorippe*, a number of Raninoid characters which, he holds, warrant the conclusion that "we have, in fact, in some of these deep-sea forms the clearest evidence of the close relation of the *Ranina* to the *Dorippe* type and quite sufficient justification for accepting de Haan's scheme of the Oxystomata, almost without modification." *Cymonomops*, however, is clearly a highly-specialised Cyclodorippid; it has been placed in this family by Bouvier, and its supposed resemblances to the Raninidæ are of the most superficial character. If the last-named family were descended from the Dromiacea it would hardly be through a Dorippid line, but it is my object to show in the following pages that the Raninidæ, though by definition they must still be included among the crabs, are not derived from a Dromiid ancestor, but have been evolved as an independent group from the Astacura. In sustaining this thesis I shall place reliance first of all on the nervous system, and secondly on the character and degree of development of the endophragmal skeleton.

Our knowledge of the nervous system of the Decapoda is not very extensive, and what we do know is due largely to the researches of Bouvier (21). He has demonstrated that the degree of concentration of the nervous system varies so considerably in the several groups of Decapoda reptantia that it cannot of itself be taken as a sure guide of affinity, but I shall be content to found my argument upon a sentence taken from his essay, 'Sur l'origine homarienne des Crabes.' "Le système nerveux des Crustacés décapodes, en effet, subit une concentration longitudinale régulière à mesure qu'on s'éloigne

des Macroures pour se rapprocher des Brachyures et la réduction qu'il présente dans le sens de la longueur, est un indice, non pas des affinités précises de l'animal, mais du degré d'évolution cancerienne auquel il est arrivé." If we accept this proposition, and for my own part I accept it without reserve, it must follow that a crab with a nervous system of which the ganglia are more concentrated in the longitudinal direction is farther removed from its Macruran ancestry than one in which the ganglia are far less concentrated, and that the former cannot be a progenitor of the latter.

Of the Raninidæ I have been able, thanks to the excellent state of preservation of the example sent me by Prof. Kishinoye, to make a thorough study of the nervous system of *Ranina dentata* and a sufficient study of that of *Lyreidus tridentatus*, of which I possessed two well-preserved examples. I have also dissected the nervous systems of *Notopus dorsipes* and *Notosceles chimmonis*, and was able to ascertain that they are of the same character and the ganglia fully as much extended in the longitudinal line as in *Ranina* and *Lyreidus*, but their state of preservation did not admit of great accuracy in making out details.

Pl. 4. fig. 8 is a drawing of the nerve-ganglion chain of *Ranina dentata*, as seen from above, the whole series being represented as flattened out in one plane. Pl. 4. fig. 9 shows the actual position of the nerve chain as seen from the side, and its relation to the endophragmal skeleton. Owing to the deep infolding of the sternal apodemes of the posterior thoracic somites, the posterior thoracic ganglia and the abdominal ganglia closely applied to them are directed nearly vertically upwards.

The cerebral ganglion is relatively large and quadrangular in outline, and the ocular, anteuinary, and antennary nerves are of large size; otherwise it does not present any special features. A small pair of nerves passes forward to the rostrum. The circum-oesophageal connectives are long and stout. The small ganglia on either side of the oesophagus give off a fairly stout nerve to dilator muscles of the oesophagus as well as the more slender connectives of the stomatogastric system. The post-oesophageal commissure is well marked. The suboesophageal ganglion mass is large and goblet-shaped in outline, as seen from above, and gives off five stout nerves on either side. These nerves are somewhat swollen at their origins, and the last two come off rather apart from the rest and give the appearance of originating from a separate ganglionic centre. Otherwise the six ganglia supplying the mandibles, first and second maxillæ, and three pairs of maxillipeds are indistinguishably fused in the suboesophageal mass. It will be noticed that the mandibular nerve does not spring from the suboesophageal ganglion but from the circum-oesophageal connectives, some way in advance of the ganglion. The ganglion pair of the chelipeds is distinct, but so closely fused to the suboesophageal mass that the connectives uniting the two are indistinguishable.

The succeeding ganglion pair, supplying the first pereopods, is situated well back in the thorax, and is connected with the pair supplying the chelipeds by two long connectives separated from one another by a well-marked interval. The ganglion-pair of the second pereopods is united with the preceding pair by similarly distinct connectives, but only one-third as long as those connecting the chelipeds and first pair. The connectives between the second and third ganglion-pairs of the pereopods are shorter, but set widely apart, leaving an oval space for the passage of the large sternal artery. The two last thoracic ganglion-pairs, supplying the third and fourth pereopods, are fused together, and the connections between them cannot be distinguished, but the separate ganglia can be clearly recognized. Closely applied to the last thoracic ganglion-pair is the chain of abdominal ganglia, completely withdrawn into the thorax and represented by a short and thick nervous mass divided by distinct transverse constrictions into five segments. The terminal segment apparently represents the fifth and sixth abdominal ganglia fused together. Paired nerves issue from each abdominal ganglionic segment, and pass backwards closely bound up in the same connective-tissue sheath as the fused mass of abdominal ganglia, but they are represented as spread out by dissection in fig. 8. The nerves issuing from the first abdominal ganglion segment can be traced to the first pair of modified copulatory abdominal limbs of the male. In this condensed and abbreviated representative of the abdominal nerve chain no trace of connectives nor of the paired structure of the ganglia can be detected. The abdominal ganglia and the nerves passing from them to the abdomen lie in the concavity of the narrow sella turcica posterior formed by the deeply infolded sternal apodemes of the last two thoracic segments. Pl. 4. fig. 10 is a representation of the ventral nerve chain of *Lyreidus tridentatus*. The general plan is similar to that of *Ranina*, but the details are different. The subœsophageal ganglion is an ovoid mass, formed by the fusion of the ganglia of the mandibles, maxillæ, and maxillipeds. As I could only count five nerves given off from this ganglion on either side, I conclude that the mandibular nerve issues, as in *Ranina*, from the circum-œsophageal connectives, but I was not able to verify this point. The ganglion-pair of the chelipeds instead of being approximated to the œsophageal as in *Ranina*, is placed further back in the thorax and is united with the subœsophageal by a thick cord, in which I could not trace any separation of the connectives in the middle line. My specimen was none too well preserved, but I can say for certain that these connectives are bound together in the same connective-tissue sheath. The ganglion-pairs of the chelipeds and first pereopods are distant and, as in *Ranina*, their connectives are separated by a distinct slit-like space. The posterior thoracic ganglia are more closely approximated than in *Ranina*, and the short connectives between the ganglion-pairs of the first and second pereopods are bound

together in the same connective-tissue sheath posteriorly, leaving only a small circular passage between them anteriorly. The connectives between the next succeeding ganglion-pairs are pretty widely divaricated to admit the passage of the sternal artery, and the last two thoracic ganglion-pairs are so intimately fused that the separate ganglia cannot be distinguished. The abdominal ganglia are precisely like those of *Ranina*, but somewhat larger in proportion to the rest of the ventral chain. In *Notopus dorsipes* and *Notosceles chimmonis* the ventral nervous chain presents much the same characters, but my examples of these species had lain for many years in spirit and were too rotten to admit of exact study. In *Notopus* the ganglion-pair of the chelipeds is separated from the suboesophageal ganglion mass by an interval somewhat shorter than in *Lyreidus*, but the connectives joining them are distinctly paired and are not included in a common connective-tissue sheath.

The above descriptions, with the figures illustrating them, show that the thoraco-abdominal nerve system of the Raninidæ approximates more nearly to the Macruran type than does that of any other Brachyuran—indeed, more nearly than any Anomuran except *Hippa*, in which genus, as I have ascertained by dissection, the thoracic ganglia are spaced fairly evenly along the longitudinal line and are united by distinctly paired connectives, except the last two which are fused together. The abdominal chain also in *Hippa* consists of at least five fairly distant ganglion-pairs united by distinctly paired connectives, but I have not yet finished my observations on this genus, and must postpone the description of its nervous system to another paper.

As compared with the Decapoda, of which the nervous systems have been accurately described and figured, the abdominal ganglia of the Raninidæ most nearly resemble the condition found in *Dromia vulgaris*, as described and figured by Bouvier (22). I have myself verified the accuracy of this description. But in *Dromia* the thoracic ganglia, though distinct, are closely approximated in longitudinal series, and form a sort of oval beaded ring round the perforation for the passage of the sternal artery, as is the case in *Culappa* among the Oxystomes, in *Corystes*, and generally in the Catametopan section of the Brachygnatha. In respect of the longitudinal concentration of the thoracic ganglia, the Raninidæ exhibit a much more primitive condition than *Dromia*. Similarly, the extended thoracic chain of the Raninidæ is in a much more primitive condition than are the approximated though distinct thoracic ganglia of *Galathea* and *Porcellana* among the Anomura, though these are more primitive as regards the abdominal chain. The same may be said in respect of *Eupagurus*, in which the thoracic ganglia are in some respects more completely fused together than in the Galatheidæ. If we carry on the comparison to the Macruran types, the Raninidæ cannot be brought into close relation with the Lobsters, and still

less with the Crayfishes, because in the first-named the thoracic connectives are separate and show but little tendency to lateral fusion. But of all the *Macrura* they most closely resemble *Nephrops* in this and other respects. In both the subœsophageal ganglion mass is in a very similar state of concentration, the differences being that in *Ranina* the mandibular nerves are given off from the circum-œsophageal connectives (this may be correlated with the great length of these connectives) and in *Nephrops* the ganglion pair of the third maxillipeds retain a certain distinctness. The connectives between the subœsophageal and the ganglion-pair of the chelipeds are very nearly of the same length and in the same condition of incipient lateral fusion in *Nephrops* as in *Notopus*, though the concentration is carried further in the lateral sense in *Lyreidus* and in the longitudinal sense in *Ranina*. The connectives between the ganglion-pairs of the chelipeds and first pereopods are much longer in the Raninidæ than in *Nephrops*, but are equally distinctly paired in both and show no tendency to lateral fusion. The same may be said of the connectives next following. In the Raninidæ the last two thoracic ganglion-pairs are more (*Lyreidus*) or less (*Ranina*) closely fused together. These differences apart, if the long chain of six abdominal ganglion-pairs of *Nephrops* were shortened up to the condition found in the Raninidæ and withdrawn into the thorax, there would be very little difference between the two nervous systems. So far, then, as this part of their anatomy may serve as a guide, the Dromiacea have progressed further from the Macrurous in the direction of the Brachyurous type than have the Raninidæ, but the latter retain many distinct Macrurous features and exhibit specially close affinities with *Nephrops*.

It will be noticed that there is a marked tendency for the thoracic ganglia to form two groups, one at the anterior the other at the posterior end of the thorax, in the Raninidæ. This must be correlated with the powerful development of the first, second, and third pereopods as digging or swimming organs. These limbs are exceedingly strong, and are actuated by largely developed muscles enclosed in remarkably deep cavities formed by the endophragmal skeleton. The size and extent of these muscle cavities as compared with those of other Brachyura is one of the most striking features when one undertakes a dissection of any member of the Raninidæ, and the abundant musculature of the limbs makes the dissection of the nervous system difficult. It is also worthy of remark that in *Lyreidus* the last pair of pereopods are very weak and attenuated and the corresponding ganglion-pair is practically unrecognizable, whereas in *Ranina*, in which the last pair of pereopods differs little in size from the rest, its ganglion-pair is distinct and emits large nerves to the limbs.

Two good figures are given in Cuvier's 'Règne Animal,' but otherwise de Haan is the only author who has dealt with the endophragmal skeleton of

the Raninidæ. He says (34, p. 136), "thoracis interior structura offert sellam turcicam uti tantum in Brachyuris, atque canalem sternalem uti in Macrouris ceterim tantum invenitur. Apodemata singula tam sterni quam epimerorum ab utraque parte medio thorace junguntur in quoque articulo sternali, canalem sternalem constituentia vertebrarumque formam plane simulantia. Apodemata cephalica pariter adsunt quinque transversa, ita ut *Ranince* hoc respectu oppositæ sunt *Dromiis*, in quibus apodemata thoracica et cephalica separatim versus centrum commune petunt." We have here a combination of Macruran and Brachyuran characters which, when the ancestry of the Raninidæ is in question, deserves close study. As a preliminary to this part of the subject, I must go in some little detail into the structure and morphology of the endophragmal skeleton. It was described both for Macrura and Brachyura by Milne Edwards (25), and since his day does not seem to have been studied in further detail. We have, subsequently, the brief but very accurate description of these structures in the Crayfish by Huxley (38). His figures, however, are not drawn from a point of view that clearly illustrates the structures described, and I shall endeavour, with the aid of new figures, to make clear some points that are necessary for a detailed comparison with the homologous structures in crabs. Fig. 11 is a ventro-lateral view of the sterna and the endophragmal skeleton of the second and third pereopodal segments of the common Crayfish, seen from the left side; the thorax has been tilted over to the right; the outlines of the articular cavities of the limbs have been thickened to make them more conspicuous. Ventrally we see the keel-shaped sternites, and at the outer side of the posterior end of each is a small articular socket, into which fits a corresponding knob on the coxa of the appropriate limb. Above are the corresponding epimera, separated from one another by a groove which is not a suture but a deep infolding of the cuticle, technically known as an apodeme. If we follow this groove down below the upper limits of the articular cavities of the limbs, we see that it bends forwards, then turns rather abruptly backwards, and seems to end just below a little knob which fits into a corresponding cavity on the coxa of the appropriate limb. Thus the articular knobs, which I shall call strophidia, are borne on prolongations of the anterior ends of the pleura, the articular cavities, which I shall call strophingia, on the posterior ends of the sterna\*. The line indicating the epimeral

\* These small articular knobs and cavities have been described in some detail, and their mechanical action has been described by Herrick (37), but though often figured, they seem to have been neglected by other authors. As I shall have occasion to refer to them frequently and to use them as landmarks, I have found it necessary to give them names, and call the socket the *strophidium*, the peg which fits into it the *strophingium*. The names are derived from the peg (*στροφίδιον*) and socket (*στροφέως*) hinge of a Greek door. For the correct formation of the diminutive *στροφέως*, *στροφίδιον*, strophidium, I am indebted to Mr. Eric Barber of Exeter College.



apodeme seems to end just below the articular knob : in reality it is prolonged beyond it, and can be traced along the inner and hinder edge of the twisted lamella or arthrophragm that separates each articular cavity from the one next behind it. The arthrophragm, in fact, is a double fold of the cuticle or apodeme, continuous with the pleural apodeme ; the two edges of the fold run down rather to the inside of the hinder edge of the arthrophragm, and in the entire animal pass respectively into the arthrodial or joint membrane of the limb in front and the limb behind. At the lower end of the arthrophragm the groove forms the apparent boundary between the contiguous sterna, but here again there is no suture ; the sterna are really continuous, and are only separated by apodemes. All this is familiar, but as separate names, epimera, sterna, arthrophragms, etc., are given to the various parts, I have thought it desirable, in view of the comparisons that are to follow, to emphasize the fact that these names only apply to local areas and indurations separated from one another by more or less deep infoldings of a continuous cuticle. In the upper and lower parts of the arthrophragm its apodeme is shallow, and consequently the arthrophragmal partition extends only a little way into the cavity of the body ; but at about the middle of its course the apodeme becomes very deep and gives rise to a lamina running upwards, forwards, and inwards towards the middle line, short of which it expands into horizontally flattened plate with jagged edges, which makes more or less intimate union with its fellow of the opposite side. The laminæ in question are the endosternites : they and their flattened summits form the walls and roof of the so-called sternal canal within which the thoracic nerve-ganglion chain lies. A sternal canal is found in the *Macrura reptantia* and in some *Anomura*, but, with the exception of the *Raninidæ*, it does not occur in the *Brachyura*. Pl. 4. fig. 11 also shows the epimeral apodemes or endopleurites. As the articular cavities slant backwards, the endopleurites alternate in position with the endosternites, and, as is familiarly known, each endopleurite divides internally, sending a posterior branch to unite with the endosternite of the segment behind, an anterior branch to unite with the endosternite in front. The result of all these complicated arrangements is that the cavity of each limb communicates internally with two imperfectly delimited chambers, which may properly be called muscle-cavities as the abductor and adductor muscles of the limbs are attached to the several apodemic ingrowths that constitute their walls. In the *Macrura*, as the articular sockets of the limbs look nearly ventrally and the epimera are not much inclined inwards from the vertical, the muscle-cavities lie in nearly the same horizontal plane and alternate with one another. A consideration of the relative positions of the dorsal strophingia and ventral strophidia by which the coxa of the limb is hinged to the articular frame will show that the outermost and slightly dorsal of the two muscle-cavities encloses the abductor muscles whose action

moves the coxa outwards, backwards, and slightly upwards; the innermost and slightly more ventral muscle-cavity encloses the adductor muscles whose action is the reverse of the abductors.

On comparing the thoracic skeleton of a crab such as *Carcinus maenas* with that of a crayfish or a lobster, the differences are considerable. The carapace being removed, the epimera are seen to slope inwards towards the median dorsal line like the roof of a house. The sterna instead of being narrow and keel-like are widely extended laterally, and form by their union the broad ventral plastron across which run a series of transverse grooves indicating the sternal apodemes. As a consequence the sockets of the limbs are placed not ventrally but on the sides of the body, forming a row which is not straight but curved upwards at both ends. In some cases the hinder end of the row curves upwards, the fourth pereopods being dorsal in position. Although *Dromia* is in many respects a primitive crab retaining many Macruran features, its endophragmal skeleton is so characteristically crab-like that it will serve for comparison and contrast with that of the Crayfish. Pl. 4. fig. 12 is a drawing of the left side of the thorax of *Dromia vulgaris* after removal of the carapace. The thorax has been slightly tilted over to the right to bring it as nearly as possible into comparison with Pl. 4. fig. 11, and for simplicity's sake the perspective of the ventral surface of the sternum has been omitted. Fig. 15 (Pl. 5) is a posterior view of the same preparation which illustrates some features not clearly shown in fig. 12.

As in *Astacus*, the strophingia and strophidia, the former situated at the upper ends the latter at the lower ends of the arthrophragms, serve as convenient landmarks. The most conspicuous feature in the crab is the great depth of the arthrophragms, especially those between the muscle-cavities of the segments of the second and third and third and fourth pereopods (intersegments xii/xiii and xiii/xiv). It is also characteristic that the three posterior arthrophragms slope forward, the two anterior arthrophragms backward, in such wise that the flexor muscle-cavities of which they form the walls converge towards a point situated in the middle of the thorax. A third characteristic feature is that, owing to the low pitch of the gabled roof formed by the epimera (see Pl. 5. fig. 15) the abductor muscle-cavities lie above and not, as in the Macrura, in the same horizontal plane as the adductor cavities. All these features, which go a long way to make up the characteristic cancrroid facies, are correlated with the habits of crabs. They run much more actively than any Macrura, and the attachments for the muscles of their pereopods are proportionally increased. To provide these attachments the intersegmental apodemes are very deep, particularly on the sternal surface and on the sides of the body, and the arthrophragms, instead of being mere flattened bars as in the Macrura, are conspicuous partitions extending deep into the body. But their internal

edges stop some way short of the middle line and are not prolonged into conspicuous endosternites. Towards their lower ends they do, indeed, give off triangular or thorn-shaped offsets (such an offset is shown in the intersegmental arthrophragm x/xi in Pl. 4. fig. 12), but these are not expanded into flattened summits and do not come into contact with their fellows of the opposite side of the body. Therefore there is no sternal canal. The epimeral apodemes or endopleurites are well-developed in crabs and, as in *Macrura*, they bifurcate at their inner ends, the anterior bifurcation uniting with the intersegmental apodeme in front, the posterior bifurcation with the intersegmental apodeme next behind, as is shown in fig. 12. It should be noted that in all these respects *Dromia* has departed so far from its Macruran ancestry and has taken on so completely the characters of crabs, that it has been possible to make use of it as a typical example of this aspect of canceroid structure.

If we now bring the Raninidæ into comparison, taking as our example *Ranina dentata*, we find a curious admixture of crab-like and Macruran characters, but the latter predominate and the former must be called deceptively crab-like, for a detailed examination shows that they must have originated independently, in relation to the habits of the animal, and not by way of inheritance from any other recognized crabs.

In the first place, as may be seen by a comparison of Pl. 5. figs. 13, 14, and 15, the contour of the thorax of *Ranina* as seen from behind is more like that of a lobster than like that of a crab. In the crab the width of the thorax largely exceeds its height; in the lobster the height clearly exceeds the width; in *Ranina* the height is rather greater than the width. Looking at the sternal surface, *Ranina* has a broad ventral plastron and in so far resembles a crab, but the most cursory inspection shows that it is made up almost entirely of the greatly enlarged and flattened sternum of the tenth segment. The more posterior thoracic sterna, particularly those of the twelfth and thirteenth segments, are narrow and keel-like; indeed, they are proportionately narrower than in the lobster. The broad sternum of the tenth segment is flat and has no vertical depth; that of the eleventh segment has the form of a pair of aliform expansions extending along the posterior edges of the twelfth sternum and making up with it the ventral plastron. Posteriorly these aliform sclerites meet in the middle line to form the short and somewhat thickened body of the eleventh sternum, tilted somewhat upward. The twelfth sternum is very narrow, of considerable vertical depth, and is curved upwards. The thirteenth and fourteenth sterna are still deeper vertically, and are so much tilted upwards that the cavities of the third pair of pereopods look nearly directly backwards and the cavities of the fourth pair look backwards and upwards (Pl. 5. fig. 14). The large articular cavities of the chelipeds are placed laterally, but those of the first

and second pereopods are almost ventral. Thus, in the middle of the thorax, the articular sockets of the limbs have the same position as in the *Astacura*, but at the two ends their position is similar to that seen in crabs (Pl. 5. fig. 17). The epimera of *Ranina* are of great depth and exhibit peculiar features that will be described later; for the moment it is sufficient to note that, owing to the size and depth of the epimera, the arthrophragms are relatively short and as in the *Astacura* are somewhat narrow curved laminæ separating the articular cavities. But, as also in the *Astacura*, the arthrophragmal apodemes are deeply extended into the body for a limited space on either side of the mid-ventral line. These extensions are the so-called endosternites, and in all the *Raninidæ* they are very largely developed, the largest of them, namely the intersegmental pair xi/xii, extending upwards as much as two-thirds of the entire depth of the thorax. As may be seen in Pl. 4. fig. 9 and Pl. 5. fig. 16, the four posterior pairs of endosternites slope sharply forwards from their points of origin from the arthrophragms, but the intersegmental pair ix/x stands nearly vertically and the pair next in front slopes somewhat backwards. The upper ends of the endosternites are widely expanded, and their innermost expansions, the mesophragms of Huxley, unite in the middle line to form the roof of a very well-marked and very deep sternal canal, at the bottom of which lies the ventral nerve-ganglion chain. This is a wholly *Macruran* character and, as we have seen, it is unrepresented in *Dromia*. In this respect, therefore, as in the nervous system, the *Dromiacea* have departed further from the *Astacuran* and have advanced further towards the canceroid type of structure than have the *Raninidæ*. The former cannot be in the direct ancestral line of the latter.

To return to a consideration of the epimeral elements of the thorax. The epimera (fig. 17), with the exception of the last thoracic, have a great extent dorso-ventrally and present features absolutely distinctive of the *Raninidæ*. That of segment ix stands nearly vertical and the broad epimeron of segment x nearly so. These two do not present any specially abnormal features, but the three succeeding epimera slope sharply forwards, so that their upper extremities converge towards the upper posterior angle of the tenth epimeron, and their extensive lateral surfaces are divided into dorsal and ventral moieties by a ridge running obliquely upwards from the hind margin of the articular cavity of the cheliped to the insertion of the abdomen. Against this ridge the lower edge of the branchiostegite fits closely and is held in position by two projections, one near the anterior edge of the eleventh, the other at the posterior edge of the thirteenth epimeron, just in front of the articular cavity of the last pereopods. The lower moieties of the epimera of the eleventh, twelfth, and thirteenth segments are therefore exposed on the surface, and form a somewhat excavated and roughly quadrilateral area between the coxæ of the limbs and the branchiostegite. The

epimeral walls in this area, being exposed, are strongly calcified. This exposure of a large portion of the epimeral surface is a remarkable and unique feature in the Raninidæ. Even in the *Astacura*, where the lower edge of the branchiostegite is free, it reaches down to the bases of the limbs, and in all crabs the lower edge of the branchiostegite is so closely adapted to the coxæ of the thoracic limbs as to leave no passage for water into the branchial chamber behind the chelæ. This peculiarity did not escape the attention of Milne Edwards, but subsequent authors seem to have paid very little attention to it. If we now examine the interior of the thorax, we find that the apodemes between the ventral and exposed parts of the three thoracic epimera in question are shallow and form nothing more than two inconspicuous thickenings internally, strengthening the framework of this part of the flanks but not projecting into the cavity of the body. But the apodemes above the line of the adherence of the branchiostegites are very deep and form well-marked endopleurites which, as usual, bifurcate and their branches unite with the expanded summits of the endosternites next in front and next behind them. It appears that the excessive depth of the sternal canal is correlated with the restriction of the endopleurites to the upper moieties of the epimera or, to put it in another way, with the downgrowth of the ventral edges of the epimera beyond the line of the attachment of the branchiostegite. The ventral extension of the epimera is an adaptive feature, and receives its explanation when the habits of the animals are taken into account. The Raninidæ are digging crabs, with large and powerful chelipeds and first, second, and third pereopods. In many the fourth pair of pereopods is weak and slender, though in *Ranina* this last pair is not much weaker than the others. The powerful digging limbs imply powerful abductor muscles and large adductor muscle-cavities. Reference to fig. 9 shows that these cavities are in fact unusually deep, and their extent is due to the great length of the endosternites within the body and to the large ventral extensions of the epimera forming their outer walls. The same figure shows that, as in crabs, the abductor muscle-cavities lie above and not alongside of the adductor muscle-cavities. But cancrioid as this character is, it has clearly a very different origin from the similar arrangement in crabs.

To turn to another feature noted by de Haan, "*thoracis interior offert sellam turcicam uti tantum in Brachyuris.*" What is this sella turcica? The name is due to Audouin and Edwards, and the latter author has described the elements entering into its composition with great minuteness on p. 34 of the first volume of the '*Histoire Naturelle des Crustacés.*' Paraphrasing his description, the sella turcica posterior is a little arch or vault, concave from side to side and convex from front to back, formed by the forward extension and fusion together in the middle line of the nearly

horizontally disposed intersegmental apodemes xiv/xv ; in other words, the apodemes separating the last thoracic from the first abdominal segment. This sella turcica is not present in all crabs, but where present the arrangements indicated above are due to the presence of a deep longitudinal mid-ventral apodeme in the last one or two thoracic sterna. The effect of this deep folding-in of the terminal thoracic sterna is to raise the hinder end of the last thoracic sternum and to throw its arthrophragmal apodemes forward into a horizontal position. The edges of the arthrophragms are thus brought into contact, and fuse in the middle line. It will be understood from the above description that the exhibition of a sella turcica is dependent on the formation of a more or less deep apodeme in the mid-ventral line of the penultimate thoracic sternum.

Figs. 13, 14, and 15 are drawings of posterior views of the thorax of the lobster, of *Ranina dentata*, and of *Dromia vulgaris* respectively. In *Homarus*—I should more correctly write *Astacus*!—the penultimate thoracic sternum is large and escutcheon-shaped in posterior view ; it has a distinct mid-ventral apodeme and the central area or inescutcheon is membranous. The terminal sternum consists of two distinct quadrangular pieces united at their inner angles, and above these is a curved transverse bar which appears to be a special calcification of the membrane connecting the last thoracic and first abdominal segment. It is not present in *Nephrops norvegicus* nor in the Crayfish (*Potamobius*). On either side of this bar the intersegmental arthrophragms xiv/xv diverge outwards to unite by slender ends with the large and peculiarly shaped epimera of the fourteenth segment. From the front edge of the sternum just where it passes into the arthrophragm of each side, the two narrow and nearly horizontal episternites run forward diverging from one another ; only their tips appear in the drawing. There is no sella turcica. In *Ranina* the penultimate thoracic segment, though relatively smaller than in the lobster, is similarly somewhat escutcheon-shaped. Both it and the ante-penultimate sternum have a deep mid-ventral apodeme, indicated by the median suture in fig. 14 and clearly shown in side view in fig. 9. The last thoracic sternum, clearly recognizable by the position of the two strophidia, is aliform with tapering wings diverging from one another and passing forwards and upwards to unite with the last thoracic epimeron. The arthrophragms xiv/xv are triangular plates arising by their bases from the front edges of the V-shaped arms of the last thoracic sternum. Their apices are, in the natural position of the animal, directed forwards and downwards ; their inner surfaces are concave and their admedian edges meet and unite in the middle line, thus forming the sides and floor of the deep trough called the sella turcica. Fig. 9 shows the relation of the abdominal nerve ganglia and the nerves given off from them to this trough. The anterior ends of the arthrophragms in question diverge from one another and, curving outwards

beyond the intersegmental endopleurites xiii/xiv, unite with the inner edges of the lower part of the endopleurites xii/xiii. The sella turcica of *Ranina* is therefore of large extent, larger than in so typical a crab as *Carcinus menas*. Among the various Brachyura that I have studied, it most nearly resembles in form and extent that of *Calappa*. But, as mentioned above, the sella turcica is not found in all crabs. Fig. 15 represents a posterior view of the thorax of *Dromia vulgaris*. The sterna of the twelfth, thirteenth, and fourteenth segments can easily be recognised by the strophidia on their outer extremities; the large pair of ventro-lateral projections in front of them belong to the eleventh sternum; their strophidia, being on their anterior face, do not appear in the drawing. The fourteenth (last thoracic) sternum does not differ much in shape from that of *Ranina* and offers resemblances to that of the lobster. The thirteenth and twelfth sterna are irregularly shaped transverse bars, of which the outer portions are calcified and distinctly separated by apodemes, but their admedian portions lose their distinctness and pass into a median membranous pouch, the walls of which are little if at all calcified. There is no trace of a median longitudinal apodeme in this membranous representative of the penultimate and antepenultimate thoracic sterna, consequently there is no sella turcica. The arthrophragms of the intersegment xiv/xv are seen converging forward from the anterior edges of the V-shaped arms of the last thoracic sternum, and in other crabs they unite above with the epimera of their own segment, in front with the arthrophragms of the intersegment in front, but in the absence of the ventral apodeme they fall far short of meeting in the middle line to form a sella turcica. In this respect, then, *Dromia* has progressed less from the Macruran towards the Brachyuran condition than *Ranina*, and this might be fastened upon as an argument in favour of the derivation of the Raninidæ as of all other crabs from a Dromiacean ancestor, but the transversely elongated twelfth and thirteenth sterna of *Dromia* are quite Brachyuran in character and very different from the narrow and keel-shaped corresponding sterna in the Raninidæ.

On the balance the evidence afforded by the structure of the hinder part of the thorax is against the Dromiacean ancestry of the Raninidæ.

Another crab in which the sella turcica is absent is *Philyra levis*. In view of de Haan's emphatic opinion that the Leucosiidæ are clearly united to the Raninidæ through *Lyreidus*, an opinion which has found favour with subsequent authors, the marked differences in the structure of the thorax demand attention. A detailed comparison of the endophragmal skeletons of the Raninidæ and Leucosiidæ is best reserved for the discussion of the possible derivation of the latter from the former family in another part of the paper, but it may be conveniently pointed out in this place that in *Philyra* the pleastron is broadest at its posterior end; the intra-sternal apodemes are nearly

transverse to the long axis of the body (with the exception of xiii/xv and xiv/xv, which are directly obliquely backwards from the middle line), are of no great vertical height, and give off no offset to form a sternal canal. The abductor muscle-cavities are of great length and slope backwards, converging to a point at the postero-external angle of the thorax on either side. There is no mid-ventral longitudinal apodeme and the arthroplegite xiv/xv is rudimentary, so there is no trace of a sella turcica. The arrangements of the several parts are as widely different as possible from those in *Lyreidus* or any other of the Raninidæ.

Though de Haan in the quotation given above (p. 33) draws a contrast between the Raninidæ and the Dromiacea in the matter of the "apodemata cephalica," i.e. the pleural and sternal apodemes of intersegments v/vi-ix/x, the Raninidæ show more resemblance to the Dromiacea than to the Astacura in this region, and the two first-named groups differ largely from the last. Passing over the obvious differences due to the presence of a broad and flat shield-shaped sternum in the Raninidæ, attention may be directed to the apodemes entering into the composition of the anterior part of the sternal canal. The reader will remember that in the Astacura, of which *Nephrops norvegicus* may be taken as a convenient example, the pleural and sternal apodemes of the three intersegments in front of ix/x, though some are missing and others feebly developed, unite to carry forward the sternal canal towards the region of the mouth. In front of them both the sternal and pleural apodemes, but particularly the latter, of intersegment v/vi are very largely developed, and their expanded internal extremities combine to form a stout platform between the subœsophageal ganglion mass and the stomach, known to the older carcinologists as the sella turcica anterior. Huxley named this platform the cephalic apodeme. In *Notopus* and *Ranina*, the only two genera of the Raninidæ in which I have been able to study these structures in detail, the endosternites and endopleurites of intersegment ix/x are normal (figs. 9, 16, & 17), the former standing nearly vertically above the plastron and ending above in slightly expanded summits which are joined in the usual way by the anterior branches of the corresponding endopleurites. The endosternites of intersegment viii/ix are small and directed backwards to touch the summits of the endosternites behind them. The endopleurite of intersegment viii/ix is minute, is not branched, and converges towards the point where endosternites viii/ix and ix/x come into contact. Intersegment vii/viii shows only rudimentary endosternites, but its endopleurites are fairly well developed, exhibiting a very short anterior branch and a posterior branch which makes connection with endosternite viii/ix. In intersegment vi/vii there is no recognizable endosternite, but the endopleurite is present in the form of a small incurved lamella. Intersegment v/vi is largely membranous, and neither endosternites nor endopleurites can



be distinguished in it. Hence there is nothing to correspond with the sella turcica anterior of the Astacura. In *Dromia vulgaris* much the same elements can be identified as in the Raninidæ, but the sternal and pleural apodemes of intersegment ix/x do not meet to form a sternal canal. Similarly the sternal and pleural apodemes of intersegment viii/ix unite on each side to form a curved shelf running inwards from the thoracic wall, but leave a wide space open in the middle line. The pleural apodemes vi/vii are fairly well developed and project some way inwards and backwards, but are far from approximating in the middle line. The intersegment v/vi is fairly stout, but is simply an arthrophragm without any ingrowths that can be distinguished as endosternites, and though the sixth pleura are well developed, they have no inwardly projecting apodemes separating them from the membrane that corresponds with the fifth pleuron. In all these respects *Dromia* has departed further from the Astacuran condition than have the Raninidæ. In another matter also, the Raninidæ stand closer to the Astacura. In the last named, for example in *Nephrops*, the ninth, eighth, and seventh sterna do not lie in the same straight line as the thoracic sterna behind them, but are directed upwards, so that a line drawn through them forms an angle of about  $140^{\circ}$  with a line drawn through the hinder ends of the more posterior thoracic sterna.

In the Raninidæ, as shown in fig. 17 for *Notopus*, a line drawn through the seventh, eighth, and ninth sterna forms an angle of  $134^{\circ}$  with a line drawn through the tenth and eleventh sterna. In *Dromia* the corresponding lines meet at an angle of  $108^{\circ}$ . This is another character in which the Dromiacea have departed further from the Astacuran type than the Raninidæ, but, as regards the six post-oral segments, it would not be quite accurate to say that they have advanced further towards the cancrioid type. There are certain points of resemblance between the Dromiacea and the Raninidæ which may be taken as evidence of but slight modification from the common Astacuran stock from which both have descended: not, however, as evidence that one group has descended from the other. The evidence so far tendered shows that the Raninidæ in their nervous system and in the characters of the endophragmal skeleton are much more nearly akin to the Astacura than are Dromiacea; they are, therefore, the more primitive group and cannot have descended from the less primitive. In both groups the departures from the Macruran type as exhibited in the first six post-oral segments are due to the acquisition of a broad sternum in the tenth segment and the upward cant of the sterna immediately in front of it, with which are associated the retreat of the sub-oesophageal ganglion mass into the thorax (see fig. 9 for *Ranina*), the decrease in length of the carapace and the increase in width of its anterior margin. The mouth is also brought to a more anterior and less ventral position than in the Macrura.

Correlated with these modifications is the extent to which the epimera of the post-oral segments are involved in the branchiostegal fold. In most of the Brachyura that I have examined they are more intimately involved than is the case either in the Raninidæ or in the Dromiacea, and the corresponding sterna and arthrophragms are modified and exhibit features departing more widely from the Astacuran type. A preliminary survey leads me to believe that a study of the structure and relations of the first six post-oral segments in the Brachyura will yield results of considerable classificatory value, but any attempt to discuss the subject would involve a long digression, and it cannot be pursued any further in this place.

But, before instituting a comparison between the pre-oral sternites and the adjacent parts of the exoskeleton in the Dromiacea and Raninidæ, it will be necessary to make a considerable digression with the purpose of clearing up doubtful points in the morphology of this region in the Decapoda reptantia, and defining more precisely certain terms which, to say the best of it, are used in an ambiguous sense by carcinologists.

In the Astacura and in Brachyura in general there is in front of the mouth a plate, usually of considerable breadth laterally, but of variable extent antero-posteriorly, to which is given the name of "epistome." Behind this is the triangular, or in Brachyura the more often quadrilateral area known as the "mouth-frame." The confusion arising from the loose application of these names is really remarkable. They are due to Milne Edwards and Audouin, and it will be well to quote the former author *in extenso* (25, vol. i. p. 251): "En arrière des fossettes antennaires, on voit une surface plane, plus ou moins étendue, qui représente le troisième anneau céphalique et qui porte le nom d'*épistome*. L'espace occupé par l'*épistome*, les fossettes antennaires et la base des antennes externes constitue ce que nous appelons la *région antennaire*. . . . Les parties latérales et inférieures de la carapace, que nous appellerons régions ptérygostomiennes, sont toujours dirigées plus ou moins obliquement en dehors et en haut, et sur la ligne médiane elles laissent entre elles un espace vide qui est occupé par l'appareil masticateur et que nous désignerons sous le nom de *cadre buccal*; tantôt ce cadre buccal à la forme d'un quadrilatère assez régulier, tantôt il est triangulaire, et c'est toujours à sa partie antérieure que viennent se terminer les conduits efférens des cavités branchiales." The definition of the "epistome" is sufficiently exact; it represents the sternum of the third cephalic segment, that is, the antennary segment. Huxley (38) calls the epistome "the sternal region which appertains, in part, to the antennæ and, in part, to the mandibles." He was correct in recognising the inclusion of the mandibular sternal element in the "epistome," so we must take the term to connote the conjoined antennary and mandibular sterna. Both Milne Edwards and Huxley further recognised the distinctness of the antennular sternum lying in front

of the "epistome." But the French naturalist, usually so exact in the definition and use of anatomical terms, goes sadly astray in the application of the terms under discussion, and has thus introduced a confusion which has persisted in carcinological literature down to the present day. Thus in vol. ii. p. 170 of the '*Histoire Naturelle des Crustacés*' we find it stated of *Dromia*, "l'épistome est triangulaire," but clearly the triangular sternal element here referred to is the *antennulary* sternum (see *infra*, p. 50). In the same place he says, "le cadre buccal est à peu près carré," and it is clear from an examination in this region in *Dromia*, that the "cadre buccal" is the combined antennary and mandibular sternum, that is, by his own definition, the epistome. Again in vol. ii. p. 97 we find it stated of the *Oxysomatous* crabs, "le cadre buccal est tout-à-fait triangulaire," and on p. 102 of the *Calappidæ*, "il n'y a point d'épistome distinct." But a study of these crabs shows that the triangular "cadre buccal" is chiefly made up of the antennary sternum, *i.e.*, it is the epistome, which is said to be absent!

Among more recent authors, Calman (23, p. 257) writes: "the antennal sternum is mainly represented by the epistome, a plate of varying shape lying between the labrum and the bases of the antennæ," and further on "the buccal frame . . . . is more or less distinctly delimited by the epistome itself or by a transverse ridge which divides the epistome into two parts, the epistome proper and the endostome or palate." He does not, with Huxley, recognise the inclusion of the mandibular sternum, but there can be no doubt that Calman identifies the greater part of the "epistome" with the antennary sternum. A little further on the same author makes the following statement: "In all the *Brachyura* the rostrum or frontal plates ends downwards in the middle line a process which unites in front of the ophthalmic and antennular sterna with the epistome and separates from one another the basal segments of the antennules." This represents accurately enough the prevailing opinion on the subject, and indicates quite clearly that the antennulary sternum is not to be regarded as a component part of the "epistome." But, whilst this part of the statement is accurate, the remaining part is most inaccurate, for an examination of a large number of crabs belonging to diverse families shows that, with very few exceptions, the downward process of the front or rostrum does not unite with the antennary sternum, that is with the epistome, but with the antennulary sternum. The fact is so obvious that it is difficult to understand how the error originated, the more so because Milne Edwards, however obscure he may have been on the subject of the epistome, is quite definite and exact on this point. "Le front se prolonge au-dessus de l'anneau qui porte les yeux. Dans le jeune âge, cet anneau reste à découvert antérieurement, et les yeux ne sont pas logés dans des cavités orbitaires complètes; mais, plus tard, la partie inférieure du front se réunit, sur la ligne médiane, à une prolongement de

l'arceau inférieure du second anneau, de façon à 'entourer complètement le segment oculaire qu'on n'aperçoit plus qu'à l'intérieur de la carapace" (25, vol. i. p. 250).

It is not necessary to push the question further, for the above quotations show that the terms "epistome" and "mouth-frame" (cadre buccal) have no definite connotation, and being incapable of exact application, must be discarded in favour of a more precise terminology founded on an appreciation of the morphological elements entering into the composition of this region. It is, however, no easy task to give such an appreciation.

A consideration of the more simple and primitive arrangements obtaining in the Macrura must precede a discussion of the highly modified relations of homologous parts in the Brachyura, and for this purpose *Nephrops norvegicus* may be selected as an example. Fig. 19 is a frontal and fig. 20 a lateral view of the cephalic segments of this species. In both the rostrum has been cut through near its base, the ocular peduncles have been cut through near their origins, and in fig. 19 the edge of the carapace has been cut away where it overlaps the external boundary of the right antennary fossa. The first point for consideration is, what constitutes the anterior extremity of the cephalothorax? Not, I think, the rostrum. Huxley (38) has given reasons for regarding the rostrum as a forward prolongation of the third or antennary somite, and although, following Milne Edwards, he based his identification on the somewhat doubtful evidence afforded by the anterior head segments of adult Stomatopods, there is no reason to go so far afield to obtain evidence in support of this view. In the deep-sea Penæidæ, *Benthescymus altus* and *Hemipeneus spinidorsalis*, the ocular and antennular segments are sufficiently distinct and freely moveable on one another to afford abundant justification for it. It is also evident from an inspection of fig. 20, that in *Nephrops* the ocular segment lies in front of the base of the rostrum and has its proper tergum in the form of a median sclerite of cartilaginous consistency, little if at all calcified, but none the less definite in form and extent and clearly recognizable as a distinct element in the exoskeleton of this region. The side-walls or epimera of the ocular segment are thin and membranous, but the sternum is a distinct triangular piece, scarcely calcified and of much the same cartilaginous consistency as the tergum. It has been recognised by all previous authors. Immediately behind the ocular is the easily recognizable antennular sternum, and to the right and left of it are the articular sockets of the antennules, separated by the arthrophragms ii/iii from the antennary sockets. The antennular segment is completed, as has been shown by previous authors, by the aliform calcified plates which form the greater part of the walls of the shallow excavations in which the ocular peduncles rest when turned outwards and represent the epimera of the antennular segment. I agree with Huxley (38, p. 157) in identifying a

narrow transverse bar at the base of the rostrum with [the tergum of the antennular segment. This bar is easily seen from the inside, but does not appear in a front view, being concealed by the base of the rostrum. Right and left of it are two deep crescentic grooves which are the external indication of two deep aliform apodemes to which the anterior gastric muscles are attached. The apodemes in question are known as the procephalic lobes, and various suggestions have been made as to their significance, but, in my opinion, they are simply the well-developed pleural apodemes of the inter-segment i/ii. Thus far the interpretations I have given are hardly, if at all, at variance with those of previous authorities, but the homologies of the antennary and mandibular segments present greater difficulties. The so called epistome of *Nephrops*, as also that of the lobster and the crayfish, is clearly made up of two parts: an anterior broad plate the lateral regions of which are produced right and left into broad divergent wings, giving the whole the shape of a broad inverted V. Behind this, fitting closely into the angle of the V, but separated from it by a distinct groove, is a somewhat projecting narrow curved bar the outer extremities of which end in incurved knobs, which knobs are excavated internally to form the strophidia for articulation with the inner articular processes of the mandibles. The presence of these strophidia is of itself evidence that the bar in question is the mandibular sternum. The transverse groove in front of it deepens in the middle line to form a triangular pit or depression and on the inner surface is a corresponding projection—in fact, an apodeme for the attachment of muscles. As transverse apodemes are always intersegmental, this groove with its median apodeme indicates clearly enough the boundary between the antennary and mandibular sterna. The antennary epimeron of either side is represented by the very narrow curved bar forming the outer boundary of the antennary socket. This bar is united by a membranous fold to and is overlapped by the fold of the anterior margin of the carapace forming the commencement of the branchiostegite. Posteriorly this bar bends inwards to form the thickened interned rim of the antero-lateral margin of the antennary sternum, and though it is completely fused with the latter, I do not doubt that this thickened rim represents the intersegmental arthropod iii/iv. Externally the antennary epimeron expands and passes, without any obvious line of demarcation, into the calcified plate marked *x* in fig. 18. In *Nephrops* this plate is firmly fused to the outer edge of the V-shaped antennary sternum, and is set back at an angle to it in such wise as to form the inner and upper wall of the anterior part of the exhalant branchial canal, but in both the lobster and the crayfish it lies more nearly in the same plane as the antennary sternum and takes little or no part in the formation of the branchial canal. The postero-internal margin of this plate is thickened, produced backwards, and engages in a groove on the front surface of the

mandible, thus forming the hinge-line about which the mandible rotates. The postero-external edge of the plate is ill-defined and passes into an imperfectly calcified area forming the roof of the branchial canal. The membrane narrows posteriorly, and arriving at the external articular process of the mandible, again becomes calcified and thickened to form a rather large strophidium for articulation with the mandible. After comparison with many other species, I have satisfied myself that the whole of this area, calcified in front and behind, but imperfectly calcified or membranous in the middle, represents the epimeron of the mandibular segment, which in the *Astacura* is fused to the antennary epimeron, but in some primitive *Brachyura*, as I shall show subsequently, is quite independent of it and also of the antennary sternum. Relying on these interpretations which, I venture to think, will be accepted by anyone who makes a careful comparative study of this region, I shall henceforth discard the misleading and purely topographical names in general use and speak of the sterna, epimera, etc., of the various segments.

Before bringing the *Raninidæ* into comparison it will be well to consider the characters presented by some other *Oxystome* crabs, particularly of the *Dorippidæ* from which, according to some authors, the *Raninidæ* are descended. I have studied *Dorippe lunata*, M. Edw., *Æthusa ciliatifrons*, Fax., and *Æthusia gracilipes*, Thiers. Of these the last-named species shows the most primitive and interesting features, and its mouth-frame and antennary region are depicted in fig. 21. The basal joints of the antennules are enormously inflated and interposed between the exposed portions of the ocular peduncles and the rostrum. The antennæ have a four-jointed peduncle and a fairly long flagellum; the basal joint is small but freely moveable. The downward process of the front or rostrum articulates with the antennular sternum, the latter being produced right and left into wings which are adapted to the shape of the inflated basal joints of the antennules. In this species the antennular sternum is largely exposed, only its posterior margin is overlapped by the front end of the spout-shaped antennary sternum. The latter sclerite is well defined and the sutures uniting it to adjacent parts can be seen clearly. It consists of a central somewhat scutiform plate with antero-external projections of which the edges are inrolled ventrally to form the spout-shaped *Oxystomatous* mouth. It is to the hinder ends of these lateral infolded projections that the pterygostomial processes of the carapace are united. Behind the body of the antennary sternum is the mandibular sternum, a very slender but distinct and calcified curved bar. Right and left, intervening between the lateral wings of the antennary sternum and the outer ends of the mandibular sternum, are two distinctly defined oval plates forming the roof of the anterior part of the branchial canal and extending so far backward that they supply the articular strophingia for

the external articular processes of the mandibles. There can be little doubt that these are the epimera of the mandibular segment, and that they are homologous with the less sharply defined areas similarly identified in the *Astacura*.

In *Æthusa ciliatifrons* the arrangements are very similar to those in *Æthusina*, but the individual sclerites are not so easily distinguished. In this species the spout-shaped anterior end of the antennary sternum is produced so far forwards that very little of the antennular sternum can be seen in a surface view. The mandibles also are reduced in size and the mandibular sternum is membranous. In *Dorippe lanata* the spout-like anterior end of the antennary sternum is produced forward to such an extent that it articulates with and overlaps the downward process of the rostrum, thus completely concealing the antennular sternum. This is one of the rare instances in which union is effected between the rostral process and the antennary sternum. In *Dorippe* as in *Æthusa* the mandibular sternum is almost wholly membranous, exhibiting only two small calcifications in the region of the strophidia. The mandibular epimera are large and distinct, triangular in shape, the apices of the triangle produced backwards. The body of the antennary sternum exhibits a large central boss in front of the mandibular sternum, which might, at first sight, be taken for a forward median extension of the latter, but it obviously has no connection with it.

After this survey of one of the families of the Oxystomatous crabs, the Raninidæ may be brought into comparison. Fig. 22 is a front view of the present region of *Notopus dorsipes*, all the appendages being removed with the exception of the right mandible and the left ocular peduncle. Fig. 23 is a similar view of *Ranina dentata*, and figs. 24 and 25 illustrate the same regions in *Notosceles* and *Lyreidus*. For descriptive purposes *Notopus*, a less modified genus than *Ranina* or *Lyreidus*, will be taken as the example of the family. The first thing to be observed is that the antennary sockets are relatively large and situated behind rather than to the sides of the antennular sockets. In this respect *Notopus* more nearly resembles *Homarus* than *Nephrops*, for in the latter the antennary sockets are displaced laterally. Reference to fig. 29 shows that in *Notopus*, as in all Raninidæ, the antennary peduncle is five-jointed, the basal joint being freely moveable, short antero-posteriorly but of relatively considerable width ventrally, and it bears the excretory aperture on a distinct prominent tubercle.

In *Notopus* and in *Ranilia*, M. Edw., the antennary flagellum is multi-articulate and of considerable length, with special features which will be referred to later. All these characters are Macruran. The antennules (fig. 28) with their enlarged basal segments and abbreviated few-jointed external and internal flagella are more canceroid in character, but the basal joints are not inflated to anything like the same extent as in the *Dorippidæ*.

and the antennary sockets lie well behind the ocular peduncles; there are no antennular fossæ internal to the orbits. The ocular peduncle of *Ranina*, as is well known, exhibits these calcified segments bent at an angle to one another when the peduncle is retracted into its orbit. Reference to fig. 22 shows that there are similarly three segments in the ocular peduncle of *Notopus*, but the two proximal are very short, the greater part of the peduncle being formed by the elongated distal segments which, when turned backwards and downwards, rests in an elongated orbital excavation fringed with hairs. There is no division of the orbit by a downward growth of the front external to the antennules, and the proximal segments of the ocular peduncles are inserted close to the middle line on either side of the rostral downgrowth. In all these respects the Raninidæ have departed very little from the Astacuran type and differ from the more canceroid characters exhibited by the Dorippidæ. In *Notopus* the downward process of the rostrum is narrow and strongly keeled ventrally; its dovetail-like articulation with the antennular sternum is well seen in fig. 22. The antennular sternum is escutcheon-shaped, strongly keeled in the middle line, and narrow posteriorly. It has a certain amount of mobility on the antennary sternum, which latter structure is a broad triangular or rather V-shaped plate the apex pointing forward, the antero-lateral margins raised and thickened but not infolded and forming part of the inner wall of the antennary sockets: more posteriorly these margins are united to the pterygostomial lobes of the carapace. The ventral surface of the antennary sternum is deeply excavated to form the exhalant orifice of the branchial canals; its anterior moiety is divided into right and left channels by a low median ridge, posterior to which the right and left branchial canals are separated from one another by a large ventrally projecting hood. This hood, which is characteristic of the Raninidæ, is the greatly developed median part of the mandibular sternum, and its postero-external corners are produced right and left into curved horns at the extremities of which are the strophidia for the articulation of the mandibles. The suture between the antennary and mandibular sternum is well marked in all the Raninidæ I have examined. The shape and size of this hood-like mandibular sternum and its relations to the antennary sternum in front and the labrum behind are shown for *Ranina* in the perspective sketch (fig. 26). The figure also shows the curved lines of hairs guarding the exit of the branchial canal; the posterior and more prominent line of hairs marks off an oblong plate forming part of the roof of the branchial canal, and as a distinct suture can be observed internally corresponding to the external line of hairs, I identify this oblong plate with the mandibular epimeron. In *Notopus* the exit of the branchial canal is guarded by a diffuse hairy patch, and the area behind this, drawn out into the triangular projection shown in fig. 22, must be taken to represent the mandibular epimeron,



but it is so intimately fused to the antennary sternum that no suture is visible.

Posteriorly the mandibular epimeron is continued into the flexible membrane forming the roof and outer wall of the branchial canal. In *Notosceles* (fig. 24) the antennary sternum is very short, is easily separable from the antennular sternum, and the intersegmental arthophragm iii/iv in front, and the mandibular epimera appear to be wholly membranous. In *Lyreidus*, on the other hand (fig. 25), in keeping with the great elongation of the pre-oral region of the carapace, the anterior part of the antennary sternum is greatly produced and to a certain extent overlaps, but does not conceal, the antennular sternum. The regions of the mandibular epimera are also produced far backwards on either side of the mandibular sternum and are calcified, but I cannot find any line of division between them and the antennary sternum. It should be observed that in *Lyreidus* the pterygostomial lobes of the carapace are produced far in front of the mandibles and are united for a considerable distance with the edges of the antennary sternum, a condition very different from that in the Leucosiidæ, with which *Lyreidus* has so often been compared.

From what precedes it is evident that the Raninidæ diverge so much from the Dorippidæ and are so much more primitive in several important particulars, that they cannot be descended from the latter family. Nor does a comparison of the pre-oral segments give any support to the descent of the Raninidæ from the Dromiacea. Fig. 27 is a frontal view of the antennary and oral regions of *Dromia vulgaris*. The antennæ and antennules have been removed and also the left ocular peduncle, but that of the right side is left in place. The whole facies is more canceroid than in the Raninidæ. The proximal ends of the ocular peduncles, concealed behind the inflated basal joints of the antennules when the latter are in place, are membranous. The antennular and antennary fossæ are small and lie in nearly the same transverse line. The orbits so far resemble those of the Raninidæ that there are no downward processes of the front external to the antennules. The median triangular shield with the apex directed forward is the antennular sternum, and evidently is what Milne Edwards called the "epistome" (*loc. cit.*). It is separated by a distinct but shallow membranous apodeme from the antennary sternum behind, and there is a certain amount of mobility between these sterna. The apex of the antennular sternum fits into a deep depression of the downward process of the rostrum, but can easily be pulled out of it. The antennary sternum forms the anterior boundary of the so-called mouth-frame, and consists of a median bilobed area and two lateral wing-shaped areas marked off from the former by grooves. The two lobes of the median area are nearly square in outline and separated from one another by a deep median fissure: their anterior margins are thickened and truncated, forming a prominent ledge behind the base of the antennular sternum.

Each of the lateral wings is armed anteriorly with a prominent spine; its outer border is nearly straight and makes nearly a right angle with the transverse ledge formed by the median lobes; its inner border is thickened and curves round the outer extremity of the mandibular sternum. The last-named structure is a projecting curved bar intimately fused to the median area of the antennary sternum, but marked off by a groove which in the middle line deepens to form a triangular fossa. Laterally the mandibular sternum seems to terminate in a pair of incurved prominences for articulation with the inner articular processes of the mandibles, but is clearly prolonged beyond these as a pair of diverging horns intimately fused to the postero-internal edges of the aliform external areas of the antennary sternum but projecting slightly beyond the latter. The mandibular epimera are largely membranous, but their antero-internal ends are calcified to form the two plates marked in fig. 26 which form the roof of the anterior part of the exhalant branchial canals. A comparison of figs. 19, 22, and 27 will, I think, convince the reader that in the whole make-up of the pre-oral region the Dromiacea have departed further from the Astacuran type than have the Raninidæ, particularly in the reduction of the rostrum, the greater development of the suborbital lobe of the carapace, the membranous condition of the inner moieties of the ocular peduncles, the size and relative positions of the antennular and antennary fossæ. Further, the modifications of the antennary and mandibular sterna are widely divergent in the two groups. It may be objected, and there would be some force in the objection, that the genus *Dromia*, on which I have relied for study of details, is a much modified and specialised genus of the Dromiacea, and that I should have directed my attention rather to the more primitive genera, *Homolodromia* and *Dicranodromia*, on which Bouvier so largely relies in establishing his theory of the Astacuran origin of crabs. Unfortunately examples of these rare and instructive forms were not at my disposal, but they have been described in sufficient detail by A. Milne Edwards and Bouvier (28), and a reference to pl. i. fig. 2 and pl. iii. fig. 2 of their admirable memoir will convince the reader that I am justified in extending the results of my study of the genus *Dromia* to the more primitive members of the group and in asserting that in the make-up of the pre-oral region, as in other characters previously dealt with, the Dromiacea have departed more widely from the Astacuran type than have the Raninidæ, and therefore cannot be enrolled in the ancestry of the latter.

I submit that, by a detailed study and comparison of the nervous system, the endophragmal system of the thorax, and the cephalic segments, I have proved the first part of my thesis and have shown that, whilst there is plenty of evidence for deriving each group separately from an Astacuran ancestor, the Raninidæ cannot be directly descended from a Dromiacean stock. The

palæontological evidence available, as far as it goes, supports this thesis. The Raninidæ are ancient forms among crabs, and when they make their first appearance have their characteristics fully developed. The earliest fossils of which I can find a sufficiently exact account are *Raninella Trigeri* from the grès verts of Maine (France) and *R. elongata* from the cretaceous beds of the Sarthe. Both deposits belong to the Turonian division of the Cretaceous. In these early Raninidæ the carapace is of elongated oval shape, broadest in the anterior third; the "buccal frame" is so much elongated that it is nearly half the length of the body; the thoracic sterna, wide between the first pair of legs, become narrowed between the second pair and are reduced to linear dimensions between the posterior pairs of pereopods; the four pairs of pereopods are compressed and adapted for digging in sand (A. Milne Edwards 27). This is the description of a very typical Raninid of fossorial habit showing no greater affinity to the Prosoponidæ or to *Protocarcinus* (*Palæinachus*, Woodw.) than do existing members of the group. The presence of *Ranina marestiana* and *Notopus Beyrichii* in the Eocene show that modern genera of the Raninidæ were then differentiated and well established. Bittner's (3) excellent figure of the latter species might pass for a representation of the anterior half of the carapace of a modern *Notopus*. Perhaps the geological evidence proves no more than the antiquity of the Raninidæ, but that antiquity affords support to the argument that they had an independent origin from the Astacura.

If, then, they are not descended from a Protocarcinid-Prosoponid stock by way of the Dromiacea, *a fortiori* the Raninidæ cannot be descended from the Dorippidæ or Cyclodorippidæ, which are themselves derived from the Dromiacea. From what has preceded it is evident that they cannot be; their primitive nervous system and endophragmal skeleton is sufficient evidence of that. On the same reasoning, the Dorippidæ cannot be descended from the Raninidæ, for it has been shown that their ancestry is altogether different. So one of the families, and that the most primitive, of the remainder of the Oxystomata is excluded from relationship with the Raninidæ. What, then, of the two remaining Oxystome families, the Calappidæ and the Leucosiidæ. They are classified with the Raninidæ because the majority of carcinologists have found it difficult to believe that the Oxystome "mouth frame" could have been acquired independently by different lines of descent. But since the Dorippidæ are excluded from relationship with the Raninidæ this objection no longer has any force. But there is room for the opinion that the Calappidæ and Leucosiidæ are descended from the Raninidæ, and I have already quoted (p. 26) de Haan's positive opinion that *Lyreidus* is an annectant form with the Leucosiidæ. There are, of course, many points of difference between the Raninidæ and the two above-named families. It would be an easy though a lengthy task

to enumerate them, but the labour may be spared because the majority of them could plausibly be explained on a theory of descent with modification from a Raninid ancestor. This explanation could be given satisfactorily in such matters as the concentration of the nervous system, the disappearance of the sternal canal, the broadening of the posterior thoracic sternum, and a large number of other characters. But it cannot apply in the case of structural features which have been profoundly altered or have disappeared altogether in the Raninidæ but are present and exhibit normal relations in Calappidæ and Leucosiidæ.

To take first a feature peculiar to the Raninidæ, the marked reduction in vertical depth of the posterior part of the branchiostegite whereby a considerable area of the epimera of the eleventh, twelfth, and thirteenth segments is left uncovered. This is by no means primitive but a definite specialisation, and I have attributed it to the burrowing habits of the family. The Calappinæ are certainly and the Matutinæ largely sand-burrowing crabs, but in both the lower edges of the branchiostegite fit very closely to the coxæ of the pereopods. In the Leucosiidæ, which are supposed to resemble the Raninidæ more closely than other Oxystomes, the adaptation of the lower edges of the branchiostegite to the coxæ of the pereopods is particularly close and elaborate. It cannot be argued that the original and more primitive relations of the branchiostegite to the epimera were re-established when the necessity for enlarged muscle-cavities for the pereopods disappeared with the assumption of new habits by the Calappidæ and Leucosiidæ, for the muscle-cavities are very large in these families but their enlargement is provided for in a very different manner. In the Leucosiidæ the arrangement of the elongated abductor muscle-cavities is peculiar and interesting, but there is no room to describe it in this place.

In all the Raninidæ the posterior margin of the pterygostomial region of the carapace is closely united to a broad offset of the tenth sternum in front of the cheliped. Consequently there is no inhalant branchial orifice in front of the cheliped, and the epipodite of the third maxilliped is aborted, though a trace of it remains in the form of a vestigial setobranch. In the Calappinæ and Matutinæ the pre-chelipedal inhalant aperture is conspicuous and the epipodite of the third maxilliped well developed. It cannot seriously be maintained that these structures have been re-acquired in these two sand-burrowing sub-families. In the Leucosiidæ, however, the posterior margin of the pterygostome is as intimately fused with the plastron as in the Raninidæ, and with the disappearance of the pre-chelipedal branchial orifice the epipodite of the third maxilliped has disappeared even more completely than in the Raninidæ, for there is not even a vestigial setobranch. A similar state of things occurs in some of the Cyclodorippidæ, but need not be discussed here because the Dorippidæ have already been excluded from

relationship with the Raninidæ. De Haan laid great stress on this point of resemblance between the Leucosiidæ and the Raninidæ, but a detail examination shows that the result is arrived at in a different manner in the two families and must be regarded as a case of homoplasy rather than homogeny. In all the Raninidæ the free end of the sternal plastron is formed by the more or less prominent lanceolate median projection of the tenth (chelipedal) sternum. The ninth sternum is narrow and projects upwards at an angle of  $130^{\circ}$  to  $135^{\circ}$  above the lanceolate projection of the tenth sternum. The coxæ of the third maxillipeds are articulated to the hinder end of the narrow ninth sternum, and therefore close to the median line, and they effectively exclude any part of the sternum from participation in the formation of the broad plastron (see fig. 27, ix). Further, in the Raninidæ, the connection between branchiostegite and plastron in front of the cheliped is effected by lateral outgrowths of the tenth sternum which meet the branchiostegal margin, not by any marked ingrowths of the latter. In the Leucosiidæ (I have studied the arrangement in *Ilia nucleus*, *Philyria undecimspinosa*, and *Philyria levis*) the ninth sternum is short antero-posteriorly, but broad and forms the anterior end of the plastron. The coxæ of the third maxillipeds are articulated to its outer ends and are therefore far apart. The tenth sternum does not give off any prominent outgrowths in front of the chelipeds, but is united to an inwardly directed process of the edge of the branchiostegite on each side, this process being the most anterior of a series of similar downgrowths of the branchiostegal margin which pass between the coxæ of the pereipods and effect the very close and elaborate fit of branchiostegite to coxæ already referred to. It may be mentioned here that A. Milne Edwards and Bouvier (28) have described a shallow pterygostomial gutter closed in below by the third maxillipeds in *Cyclodorippe*. This gutter occupies the same position as the well-known pterygostomial inhalant canal of the Leucosiidæ, and the similarity of the structural appointments is so great as to suggest the derivation of the Leucosiidæ from a *Cyclodorippid* rather than from a Raninid ancestor.

Finally some importance is to be attached to an apparently minor feature. In all the Oxystomatous Crabs the floor of the exhalant branchial canal is formed by an expanded spoon-shaped operculum furnished by the first maxilliped. In the Raninidæ (see figs. 31, 45, 50, & 53) both the exopodite and endopodite are expanded and modified, and co-operate in forming the operculiform floor in question, but it is the exopodite which is the longest, most expanded, and the most effective agent in forming the operculiform floor of the anterior part of the exhalant canal. This modified exopodite never bears a flagellum. In the Leucosiidæ, the Calappinæ, and the Matutinæ (Garstang is in error in stating that the exopodite is operculiform in *Matuta banksii*) it is the endopodite of the first maxilliped that is elongated,

expanded, and modified to form the operculiform floor of the exhalant canal. The exopodite is somewhat modified and to a varying extent in different genera, but it is always shorter than the endopodite, does not share in the formation of the operculum, on the whole retains the characteristic shape of an exopodite, and invariably bears a flagellum—I hope I may not be criticised for attaching undue importance to a trifling character. It is just such instances as this, in which the same purpose is effected by somewhat different means, that afford the best criteria as to whether some particular structural resemblance is homogenetic or homoplastic. It was the discovery of this difference in the structure of the first maxillipeds that finally confirmed my opinion that the Raninidæ are not genetically connected with the other Oxystomatous Crabs. My reliance on this item of evidence was somewhat shaken by A. Milne Edwards and Bouvier's statement that the opercular floor of the exhalant canals in *Cymonimus* is formed by the dilated exopodites of the first maxilliped, but an examination of their figure (28, pl. xv. fig. 6—there is a mistake in the numbering of these figures—) shows that the resemblance to the Raninidæ is only superficial, and the exopodite of the first maxilliped of *Cymonimus* has a long six-jointed flagellum furnished with long setæ. My test case, therefore, holds good, and the evidence produced is sufficient to justify Boas' doubt as to the inclusion of the Raninidæ among the other Oxystomata, and A. Milne Edwards and Bouvier's decision to exclude them from their monograph on the Oxystomata of the 'Blake' and 'Hassler' Expeditions. The Raninidæ, therefore, must be removed from their present systematic position and assigned to some other place in classification. They cannot be excluded from the section Brachyura for reasons given on p. 27, but in conformity with more recent and generally accepted classifications they must rank as a separate tribe, equivalent to the Dromiacea, Brachygnatha, and the rest of the Oxystomata. For this new tribe I propose the name **Gymnopleura**\*, which directs attention to one of the most characteristic features of the group, namely the exposure of the epimera of the posterior thoracic segments. This new tribe may be defined as follows.

### Tribe **GYMNOPLEURA.**

Anterior thoracic sterna broad, posterior thoracic sterna narrow and keel-like; posterior thoracic epimera largely exposed by reduction of branchiostegite; female openings on coxæ; last pair of pereopods dorsal in position,

\* Mr. T. R. R. Stebbing in 'Nature,' Jany. 1922, has pointed out that Latreille (Cours d'Entomologie, 1831) instituted the tribe *Notopterygia* for *Ranina*. At first sight it seemed advisable to adopt Latreille's name for the tribe comprising the Raninidæ instead of my own. But the rules of nomenclature do not apply to tribal names; Latreille's system of classification differs largely from that followed in this paper and his reasons for placing *Ranina* in a separate tribe differ widely from mine. Confusion rather than perspicuity would result from the adoption of Latreille's tribal name.

normal or reduced in size ; sternal canal present ; thoracic nerve ganglion-chain elongate ; antennary sternum triangular, spout-shaped ; branchiæ 8 on each side. . . . . FAMILY : *Raninidæ*.

We may now deal with some features of general and special interest presented by the tribe *Gymnopleura*. It has been shown to have originated, independently of other "crabs," from the *Astacura*. It is but a small assemblage of animals, comprising some eight or nine living genera, exhibiting a very small range of variation, and evidently very well adapted to their environment, for the tribe emerges in the Cretaceous with its special adaptive characters fully established, and two of the recent genera date back to the Eocene. But although not descended from crabs, but from lobsters, the *Raninidæ* have been so similarly modified, in one direction and another, that they must be classed with the crabs with which they have no relationship save that of a remote common ancestor which was not itself a crab. It is by no means an isolated phenomenon. We know of several crab-like forms, *Porcellana*, *Lithodes*, *Hippa*, and the interesting *Porcellanopagurus*, whose assumption of a crab-like form has been described in a very lively manner by Borradaile (20), which have undoubtedly been derived, quite independently in each individual case, from Macrurous ancestors. The question is, what causes have operated to produce so great similarities in animals so remotely related to one another? Without doubt, I think, the answer is that the efficient cause has been the assumption of the habit of burrowing in sand or mud. Bohn (7) has shown that various members of the *Nephropsidea*, when living on sandy bottoms, protect themselves by an investment of sand, and to a limited extent take cover in it. But their pereopods are ill-adapted for digging ; they must retreat backwards into the sand to leave their antennæ and eyes free to keep watch against enemies, and the elongated abdomen is a great obstacle to the effective and rapid concealment of the posterior parts of their bodies. A suitable modification of the pereopods and reduction and infolding of the obstructive abdomen are prerequisite to retrofossorial efficiency, and any mutations in these directions must have had a high selective value. It is not surprising that favourable modifications should have presented themselves and have been selected several times over, nor is it surprising that, once the burrowing habit was adopted, similar adaptive modifications to the new condition of life should have established themselves. In the first place the Decapod, buried in sand or mud, must adapt its respiratory mechanism to the changed conditions. The inhalant spaces extending along the posterior and ventral edges of the branchiostegite would be choked and rendered useless unless some provision against the entrance of sand were developed, and the researches of Garstang and Bohn have shown by what various means this form of suffocation is obviated in different genera of the sand-burrowing

crabs. Most commonly the edges of the branchiostegite are fitted closely to the epimera just above the coxæ of the pereopods and to the tergum of the first abdominal segment, so that no water can find ingress or egress that way. As a consequence the podobranchs or arthrobranchs of the three posterior pereopods disappear; there is no longer room for them, and as the branchial cavity is reduced posteriorly by the great development of the muscle-cavities of the digging legs, the posterior pleurobranchs follow suit. The branchiæ are reduced in number and those that remain are massed in the anterior half of the branchial cavity, nearest to the newly developed entrance of the respiratory current in front of the chelipeds. In the Raninidæ, however, the arrangements differ from those usually observed in crabs. There is, in most of them, a pair of posterior respiratory orifices situated between the tergum of the first abdominal segment and the coxæ of the last pair of pereopods. When the abdomen is extended or only slightly flexed, water can pass freely into or out of these orifices, but they are pretty effectively closed when the abdomen is closely flexed under the thorax. The orifices were accurately described and figured in *Ranina* by Milne Edwards, but many subsequent authors, particularly Ortmann (42), seem to have failed to recognise them. Borrodaile (14) gives an accurate account of their relations. These posterior branchial orifices are not, however, peculiar to the Raninidæ: I have found them in precisely the same position in *Corystes*, in which genus they can easily be seen by bending the abdomen upwards and looking between the lower side of the tergum of the first abdominal segment and the coxa of the last pair of legs. Garstang (30) failed to observe these apertures in *Corystes*, and I suspect, but have not yet had the opportunity of proving it by experiment, that they form the main entrance for water into the branchial chamber during the operation of the normal current. There is also a pair of posterior apertures in *Thia polita*, but these are in a somewhat different position, close under the edge of the branchiostegite in front and to the outside of the articulation of the first abdominal segment with the carapace, and well in front of the coxæ of the last pair of pereopods. The persistence of a posterior branchial opening is a primitive feature, never to be seen, as far as my observations go, in crabs in which the abdomen is permanently flexed and kept closely applied to the sternal plastron.

To return to the Raninidæ: the posterior part of the branchial chamber, into which the posterior orifice opens, is reduced to a narrow passage by the reduction in vertical depth of the branchiostegite and the close adherence of its edge to the thoracic epimera. The edge of the branchiostegite is held in place by two prominences, one on the anterior edge of the eleventh, the other on the posterior edge of the thirteenth epimeron, and a close fit is ensured by a well-marked ridge running upwards and backwards along the eleventh, twelfth, and thirteenth epimera (figs. 7 & 17). Thus the entrance of water into or its egress from the branchial chamber at the sides of the



thorax is effectively prevented. The only entrances and exits are by way of the anterior so-called exhalant branchial canals and by the posterior canals described above. Böhn (6) has shown that reversal of the respiratory current, first observed in *Corystes* by Garstang, is a normal phenomenon among Decapod Crustacea, and is manifested even when they are buried in the sand. There must, therefore, be some apparatus in forms which, like the Raninidæ, have posterior branchial orifices for filtering the sand from the water entering by these orifices during the "normal" phase of the respiratory current; that is when it is setting from behind forwards. In most of the Raninidæ, notably in *Ranina*, *Notopus*, *Notopoides*, *Notosceles*, and *Zanclifer*, this apparatus is furnished, partly by the chelipeds, but principally by the manner in which the flattened pereopods, the edges of which are fringed with long and closely set hairs, are bent upwards and forwards in such a manner as to form a water-chamber on either side of the posterior thoracic segments. The part played by the pereopods would never be guessed from the conventional representations of these animals in systematic works, where they are depicted, usually from the dorsal surface, with the legs extended symmetrically on either side of the body in order to display as much as possible of their structure and the chelipeds extended forwards in front of the body. The adaptive characters of the thoracic limbs can be studied with equal advantage in *Notopus*, *Notopoides*, *Zanclifer*, *Notosceles*, and *Ranina*, but I will take the last-named genus as an example for descriptive purposes.

In *Ranina* there is a conspicuous triangular patch of short dense hairs extending forward from the articulation of the cheliped over the postero-lateral area of the pterygostomial region on either side of the thorax. The conjoined basis and ischium of the cheliped is very short and immoveably fused to the merus, the two forming a relatively long curved segment of the limb, dilated on its external aspect but smooth and flattened internally so as to fit closely against the hairy patch on the pterygostome. It is evident, from its smooth and polished inner surface, that the ischiomerus is normally held close to the body and slides forwards and inwards or outwards and backwards over the above-mentioned hairy patch. Whatever its position, so long as it is pressed against the hairy patch, there is no room for the passage of water, much less of sand or mud, between it and the pterygostome. When the ischiomerus is rotated as far forward as possible, the somewhat inflated carpus lies beneath the outermost of the large frontal spines of the carapace, and the flattened propodus and dactylus are folded back under the anterior part of the pterygostomial region, but do not fit closely and accurately to the latter as in the case of *Calappa* and *Matuta*. Their function is quite different. It is evident that instead of forming the floor of what Garstang has called an exostegal canal the propodus is so articulated to the carpus that without either the latter or the ischiomerus being shifted from their positions, it can be rotated outwards in such a manner as to rake

sand or other material from beneath the anterior part of the carapace, the raking action being facilitated by the five large spines on the lower margin of the propodus. Thus a more or less clear water-way is kept on the under side of the anterior side of the thorax.

When the ischiomerus is drawn as far back as possible, the carpus can be flexed inwards to form an acute angle with it, and the flattened propodus may then be folded back so far that its posterior margin fits into a groove in the merus and both it and the dactylus are pressed against the basal joints of the third maxillipeds. In this position also the propodus can be rotated outwards with a raking action so as to clear away sand from beneath the body, without any corresponding movement of the ischiomerus and carpus. A close examination of the chelipeds leaves no doubt that their main function is to keep open a passage for water down to their basal joints. From this point backwards water must pass in two streams to the posterior branchial orifices along passages roofed in, partly by the overhanging edges of the branchiostegite, partly by the forwardly directed last pair of pereopods. The inner walls of these passages are formed by the epimera of the eleventh, twelfth, and thirteenth segments, which are somewhat excavated and overhung by the edge of the branchiostegites. Their outer walls are formed by the first three pairs of pereopods, which are tucked up under the roof formed by the last pereopods, the merus in each case being directed forwards, the carpus, propodus, and broad lanceolate dactylus downwards and backwards. The segments of the pereopods being broad and flattened and their margins furnished with fringes of stiff closely set hairs, they form a sort of basket-work or sieve the meshes of which are filled in by the fringes of hairs, and the whole apparatus is adapted to admit to the interior water from which sand and other solid particles have been strained. The strainer is made more effective by the dense hairy fringes on the edges of the branchiostegite, and the whole apparatus is completed and roofed in posteriorly by the flattened segments of the abdomen, which are likewise provided with dense fringes of stiff hairs.

Whatever may be the position of the chelipeds, there is a ventral gap on either side between their basal joints and the first pair of the pereopods. This gap is partly filled by the "epaulettes" projecting from the sterna of the eleventh segment; the rest of the gap is bridged over by the stiff hairs projecting from all round the margins of the epaulettes and forming a very effective strainer. It is through these two gaps furnished with this efficient straining apparatus that the greater part of the respiratory current of water must find its way from the cavity raked out in the sand by the chelipeds underneath the anterior part of the thorax.

The structure and arrangement of the pereopods and their relations to the thoracic epimera and abdomen being as above described, it may be inferred that *Ranina* buries itself in the sand by the digging action of the

first three pairs of pereopods, the fourth pair being used to shovel the displaced sand outwards. When dug in, the animal may be inferred to assume an oblique position, the frontal spines of the carapace just breaking the surface of the sand; the chelipeds are folded up under the pterygostomial region of the carapace and the long three-jointed eye-stalks may be extended well above the sand on the look-out or, on the approach of danger, may be folded back and concealed in the orbital cavities. In this position the normal respiratory current will be provided for by the raking action of the chelipeds and the lateral water-passages enclosed between the pereopods and the thoracic epimera, as described above. These afford a mechanism whereby filtered water is supplied to the posterior branched openings, and the normal exhalant current will pass out by the narrow anterior passage bounded below by the merus of the third maxilliped and laterally by the flattened basal joints of the second antennæ.

As the Raninidæ are tropical and sub-tropical crabs living at considerable depths it has not been possible for me to observe the habits of the living animals, much less to make experiments on their respiratory mechanisms. But in the absence of direct evidence I consider myself justified in giving the foregoing account of the course of the normal respiratory current, the more so because an examination of numerous specimens of *Notopoides latus* and of several examples of *Zancelifer caribensis* in the British Museum of Natural History gives the clearest evidence that these species are sand burrowers, and that an inhalant current passes into their branchial chambers through the posterior branchial orifices, which are exceptionally large and conspicuous in these cases. In nearly all the individuals of these two species the conspicuous hairy fringes of the pereopods, of the abdominal pleura, of the edges of the branchiostegite, and of the epaulettes of the eleventh sterna, are more or less heavily clogged with sand, a fact which bears witness to their function as a filtering apparatus. On the other hand, the water-passages lying between the posterior thoracic epimera and the pereopods, and therefore guarded by these hairy fringes, are remarkably clean and free from sand. The filtration, however, has not been perfect, for the walls of the posterior branchial passages are encrusted with fine particles of sand, the distribution of which leaves no doubt that the current which deposited them set in from behind forwards. The evidence in these two species is remarkably clear, and the inferences drawn from it may be extended to *Notopus dorsipes* and to *Notosceles rhimmonis*, though, in the last-named species, in which the last pair of pereopods are greatly reduced in size, there is evidence that the posterior inhalant respiratory current is becoming of less importance and that the incurrent supply of water to the branchial chamber is chiefly provided for by special modifications of the antennary region.

In the absence of opportunities for observation of and experiment on living

animals, the exact course of the anterior inhalant respiratory current in the Raninidæ must remain largely a matter of conjecture. Nevertheless I have not hesitated to put forward the following interpretation based upon a detailed study of anatomical facts in the hope that, whilst my conclusions must necessarily be subject to revision and correction, naturalists who have opportunities of studying the live animals may be so far interested as to devote some time and trouble to the elucidation of the workings of their respiratory mechanisms. The anatomical characters are most easily studied in *Notopus dorsipes*, and it is probable that what is true of this species is also true of *Ranilia muricata*, M. Edw., but as I have only been able to examine a single dried example of the latter in the British Museum of Natural History, I cannot say anything certain about it. I have stated elsewhere (p. 26) that, in my opinion, *Ranilia*, M. Edw. = *Notopus*, de Haan. In *Notopus* the antennæ are more primitive, that is to say, they depart less from the Macruran pattern, than in any other Raninidæ. The peduncle (figs. 29 & 29a) is made up of five distinct segments of which the proximal is admedian in position, small, largely concealed by the sub-antennary lobe of the pterygostome and bears at its inner angle the aperture of the excretory gland. The second segment is also small and largely concealed by the sub-antennary lobe: it lies on the same level as the first and is external to it. The third segment is large, sub-quadrangular in outline, its extero-ventral surface slightly convex and tuberculated, its intero-dorsal surface smooth and slightly concave. Its admedian margin is prominent and curved, forming a projection which meets its fellow in the middle line. It bears a conspicuous tuft of long forwardly directed setæ. Its extero-anterior angle is produced into a process which embraces the proximal part of the fourth peduncular segment; this process is largely developed in other Raninidæ but remains small in *Notopus*. The fourth and fifth segments are fairly long, their external and ventral surfaces granular and convex, their admedian surfaces smooth and flat or slightly concave. The dorsal and ventral edges of these smooth admedian surfaces are fringed with long closely set plumose setæ which, when the two antennæ are approximated, interlock with the corresponding setæ of the antenna of the other side. The antennary flagellum comprises twenty-six joints, is relatively longer than in any other Raninidæ (except *Ranilia*, M.-Edw. and *Cosmonotus*) and bears a dorsal and a ventral row of strong setæ which are directed obliquely inwards so as to interlock with those of the opposite side when the antennary flagella are approximated. Thus there is formed an antennary water-tube (figs. 1 & 56), shorter indeed but otherwise similar to and fully efficient as that of *Corystes*. Water sucked down the antennary tube passes into a shallow chamber lying behind the bases of the antennæ, the floor of which is formed by the meri of the third maxillipeds, its roof by the spoon-shaped expanded anterior ends of the exopods of

the first maxillipeds. These last are concave dorsally and convex ventrally, and fit so closely and accurately to the converging exhalant channels of the antennary sternum as to constitute an efficient horizontal partition between an exhalant passage above and an inhalant passage below. The incurrent stream of water, taking the more ventral course, must pass right and left along the conduits provided by the grooves on the ventral sides of the exopods of the second maxillipeds; thence under the edge of the inflated pterygostome into the channel which lies parallel to that in which the scaphognathite works, but separated from the latter by the vertical partition formed by the mastigobranch of the first maxilliped. The floor of these inhalant passages is formed by the flat and closely opposed meri and ischia of the third maxillipeds the outer edges of which fit close to the mouth frame. There is no "exostegal" groove in the pterygostome forming a definite inhalant canal as in the Leucosiidæ, but the relation of the incurrent to the excurrent stream of water must otherwise be much the same in the two groups. That is to say, in both cases there must be two opposite currents, the one setting inwards to, the other setting outwards from the antennary region of the front.

In both the Raninidæ and the Leucosiidæ the excurrent stream is set in motion by the "normal" action of the scaphognathite, and passes forward between the converging channels of the antennary sternum and the exopods of the first maxillipeds to emerge between the basal joints of the antennules. The course of the incurrent stream in the Raninidæ is as described above for *Notopus*, but it can hardly have escaped the reader's attention that the channels in which the opposite currents flow are not very distinctly separated from one another. In the Leucosiidæ the existence of the exostegal canals makes the separation much more complete, and the respiratory mechanism is in this respect more highly specialised than it is in the Raninidæ. In this connection it should not be forgotten that the latter have additional apertures of ingress to the branchial chambers, viz., the posterior branchial apertures of which there is no counterpart in the Leucosiidæ.

It may be surmised that *Notopus* makes use of the posterior branchial apertures only when it is lightly covered by the loose upper stratum of sand, and can make use of the raking action of the chelipeds to clear a passage for water below the thorax. As it digs down into the more compact deeper layers of sand, this source of water-supply must become more and more restricted, and the antennary tube is then brought into action. It is of course possible and even probable that, when the antennary tube is used, the action of the scaphognathite is reversed and the posterior branchial apertures become exhalant, the frontal exhalant passages being closed and thrown out of action so long as the respiratory current is reversed, only to be brought into use again when the normal respiratory current, from behind forwards, is restored. But the evidence is strongly in favour of my contention.

that in the *Raninidæ* an anterior incurrent stream of water is produced by the "normal" action of the scaphognathite.

In no other member of the group (with the possible exception of *Cosmonotus*, which I have not had the opportunity of studying sufficiently closely) do the flagella of the antennæ form a water-tube as in *Notopus* and *Ranilia*. Indeed, the antennæ are modified in other directions but, none the less, are subservient to the establishment of an inhalant water current, the course of which can best be described by taking *Ranina* as an example.

In this genus both the antennæ and the antennules are modified in connection with the respiratory currents. The antenna (figs. 35 & 35 a) is short and thick, the flagellum reduced to a rudiment comprising at the most seven joints; often it is missing. The two basal joints of the peduncle are fused together, but the suture between them remains distinct. The first joint is triangular in outline, with the apex directed forward; its admedian basal angle projects inwards and slightly forwards and the excretory aperture is placed somewhat to its dorsal side, in such a position that the excretory products are discharged into the excurrent rather than into the incurrent stream. The two basal joints, which have a very limited movement in the antennary socket, lie directly in front of the sub-antennary lobe of the pterygostome, but the third peduncular segment is flexed inwards to form a somewhat acute angle with them. The shape of the third segment can best be understood by reference to figs. 35 and 35 a, which represent external and admedian views of the right antenna. The most noticeable feature is the great development of the external lobe. Small and inconspicuous in *Notopus*, this lobe in *Ranina* forms a large sinuous ridge which projects forward as far as the anterior limit of the fourth segment; its outer margin is fringed with long plumose setæ. When the third peduncular segment is flexed towards the middle line, the lobe in question is brought into a position athwart the incomplete lower boundary of the orbital cavity, and forms its ventral and internal wall, the long fringe of hairs on what is now its anterior margin extending upwards across the orbital cavity and interlocking with a similar fringe spreading downwards from the supra-orbital ridge of the front of the carapace. For brevity's sake this lobe will be referred to as the crest of the third peduncular segment. The fourth segment is sub-triangular in section: its external and ventral surfaces are convex and granular, but its internal surface is smooth, slightly concave, and flabelliform in outline. Its margins are surrounded with long plumose setæ the disposition of which is shown in fig. 35 a. The fifth peduncular segment is small and the flagellum rudimentary or absent. When the antennæ are flexed inwards, the concave flabelliform surfaces of the fourth segments are brought nearly into contact in the middle line, their marginal setæ interlock, and thus a narrow but deep space is enclosed which is continued posteriorly into the wider space bounded

laterally by the smooth and somewhat concave inner surfaces of the third peduncular segment; ventrally by the meri of the third maxillipeds; dorsally by the densely setose exopods of the first maxillipeds. This may be called the inhalant chamber.

The antennules are inserted to the inside of and somewhat above the antennæ. As shown in figs. 34 and 34 a, their basal joints are expanded distally into a flabelliform lobe very similar to that of the fourth peduncular segment of the antennæ and, like the latter, their margins are garnished with a fringe of long setæ. The slightly concave inner surfaces of these flabelliform expansions of the antennules, when opposed in the middle line, form a second vertical cleft or passage within the larger passage formed by the antennæ, and this internal and somewhat dorsal antennular passage is so disposed that its hinder opening coincides with the spout formed by the convergence of the exhalant canals of the antennary sternum. The cleft between the basal joints of the antennules therefore serves as a conduit for the excurrent stream of water. Thus far the apparatus for directing the courses of the excurrent and incurrent respiratory streams differs from that of *Notopus* chiefly in the fact that in *Ranina* the long tube formed by the antennary flagella is absent, but in the latter genus a large part of the incurrent stream must find its way into the above-mentioned inhalant chamber through the orbital cavities. I have already shown how these narrow and elongated cavities are covered in by fringes of setæ which meet over the retracted eyes and eye-stalks but are pushed aside when the latter are extended. Though the orbit appears to be closed below by the crest of the third segment of the antennary peduncle, a sufficiently wide space is left between this segment and the basal joint of the antennule to allow of the free passage of water from the orbit into the inhalant chamber, and much of the inhalant current must pass through the orbits. It is evident that when the animal is deeply dug in, the broad front of the carapace just breaks the surface of the sand; the tips of the largest frontal spines perhaps project very slightly above it. The hairy fringes of the orbits and of the fourth joints of the antennæ are then just awash between sand and water, and are admirably adapted for filtering solid particles from the streams setting inwards through the orbits and between the flabelliform fourth segments of the antennæ. Water is also admitted into the orbits on either side through a considerable cleft lying between the long and narrow sub-orbital lobe of the pterygostome and the innermost of the large frontal spines. These clefts are guarded by dense hairy fringes. The arrangements by which the incurrent stream is directed from the inhalant chamber into the branchial chamber by the channel formed by the exopod of the second maxilliped are the same in *Ranina* as in *Notopus*.

I would not have presumed to give an account unsupported by direct

observation and experiment of such complicated functions as those dealt with in the foregoing paragraphs if there were not very clear evidence that such an anterior inhalant current as I have described does in fact exist. One such piece of evidence is afforded by the matted feltwork of hairs covering the ventral surfaces of the expanded anterior extremities of the exopods of the first maxillipeds. These hairs lie flat and point backwards: they are as evidently laid back by a current of water passing over them as the sea-grass on the mud-banks of an estuary is laid back by the tide that has swept over it. Again, in most examples of *Ranina* a considerable amount of sand is entangled in the setæ with which both the exopods and endopods of the second maxillipeds are abundantly furnished. This gives evidence that these appendages are bathed by a current of water not wholly freed from sand-particles by the filtering apparatus of the orbits and antennæ. But perhaps the clearest evidence of all was furnished by the large *Ranina* sent me by Prof. Kishinoye. In this specimen the inner surfaces of the third peduncular segments of the antennæ, the ventral surfaces of the exopods of the first and second maxillipeds, the inner surfaces of the mastigobranchs of the first maxillipeds, the proximal part of the mastigobranchs of the second maxillipeds, and the bases of the podobranchs of the second and third maxillipeds were infested by numerous small pedunculate cirrhipedes belonging to some as yet undetermined genus and species of the family Lepadidæ. In other words, these intruders had established themselves along what I have described as the course of the incurrent respiratory stream, but none were to be found in the upper part of the gill-chamber, nor on the scaphognathite, nor on any part of the walls of the exhalant canals. It is evident that their larvæ had been swept by the incurrent stream into the inhalant chamber, and had subsequently fixed themselves in positions where the adults could obtain a constant supply of nourishment borne by the incoming current. But, where the currents were setting outwards, conditions were unfavourable and none had established themselves.

From what precedes, it follows that *Ranina*, no less than *Notopus*, is highly adaptable in respect of its respiratory arrangements, and can make use of different mechanisms as the circumstances of the moment may require. When half buried in loose sand or when wandering on the surface these animals probably respire through the apertures at the posterior end of the thorax. When deeply buried in compact sand they are forced to rely on the antennary apparatus. In point of efficiency and specialisation their respiratory mechanisms fall far short of those exhibited by other "Oxystomatous" crabs, the Leucosiidæ, the Calappinæ, and the Matutinæ, but adaptability to varying conditions implies a high survival value, and it is to be remarked that *Notopus* and *Ranina* are among the oldest of the fossil Raninidæ.



Among other genera, *Zanclifer* and *Notopoides*, though their antennary flagella are not so much reduced, are in all essential respects so similar to *Ranina* that it can hardly be doubted that they have similar habits and are equally adaptable as regards their respiratory processes. *Zanclifer* differs from all other Raninidæ in having normal, *i.e.* not feathered and differentiated, chelipeds, and it may be that it is more nearly related to the ancestral form than *Notopus*. It has all the external characteristics of a burrowing crab. *Notopoides*, on the other hand, is much more closely related to *Notopus*, from which it differs mainly in the elongation of the twelfth sternum, whereby the second, third, and fourth pereopods are shifted backwards and form a posterior group of legs, separated by a space from the first pereopods: this feature is exhibited to a more marked degree in *Notosceles* (fig. 3) and is carried to an extreme in *Raninoides* (fig. 6). In each genus the increase in length of the twelfth sternum is correlated with a reduction in size of the last pair of pereopods, a progressive narrowing of the abdomen, a reduction in the size and functional importance of the posterior branchial orifices, and progressive modifications of the second and third pereopods indicative of their increasing use as swimming organs. A comparison of the series *Ranina*, *Notopus*, *Notopoides*, *Notosceles*, *Raninoides*, leads me to the conclusion that, whilst all of them are to a greater or less extent sand-burrowers, the first-named during its periods of activity progresses mainly by crawling and is a poor swimmer. *Notopus* and *Notopoides* crawl and swim; *Notosceles* is a fairly efficient and *Raninoides* a very efficient swimmer. This conclusion I will now endeavour to justify.

*Notopoides* is obviously a burrowing crab; the sandy condition of the specimens in the Natural History Museum bears testimony to this habit. In most of the structural features subservient to the respiratory processes *Notopoides* bears a strong resemblance to *Notopus*. Attention may be directed specially to the following points: the last pair of pereopods are not much reduced in size and all their joints are densely fringed with hairs; the tergum of the first abdominal somite is as broad as the posterior margin of the carapace; the posterior branchial orifices are patent and give evidence of their function as inhalant passages; the exposed portions of the epimera of the eleventh, twelfth, and thirteenth somites are concave and overhung by the edge of the branchiostegite; the chelipeds are adapted for raking sand from under the thorax. In short, all the adaptations described in *Notopus* and *Ranina* for maintaining a respiratory current through the posterior respiratory orifices are present to an equal degree in *Notopoides*. This genus must be equally addicted to the burrowing habit, but the articulations and characters of its last three pairs of pereopods suggest that, when active, it is to some considerable extent a swimmer.

In *Notosceles* the adaptations for maintaining a posterior inhalant respiratory current are still recognizable, but are obviously less efficient.

The last pair of pereopods, though much reduced in size, is sufficiently liberally provided with hairy fringes to form an effective covering for the roof of the water-chambers enclosed between the other pereopods and the thoracic flanks. The opimera forming these flanks, however, are not so deeply concave as in *Notopoides*, and the posterior branchial orifices, though distinct enough, are smaller and obviously of less functional importance. The dactylus of the last pair of pereopods is small, elliptical, and clearly better adapted for natation than for digging.

Before entering into a discussion of the transition from digging to swimming limbs it should be premised that in the pereopods of all the Raninidæ the articulation of the dactylus to the propodus is singularly like that of the tarsi of the whirligig-beetle *Gyrinus*, familiar to all naturalists from the illuminating description of Miall. Generally, in the Raninidæ, the carpus is moderately long, triangular in shape, with an extensive basal articulation for the propodus. The propodus is a short and broad oblong, more or less flattened, with a very small articulation for the dactylus close behind its postero-external angle. The dactylus is very variable in shape. Generally in the first two pereopods it is lanceolate and obviously efficient in digging, but in the last two pereopods something between crescentic and cleaver-shaped like an oriental "kukri." In either case it is so articulated by a narrow pedicle to one end of the oblong propodus that it can be slid behind the latter as the sticks of a lady's fan slide over one another. A very similar form of limb with yet more elaborate adaptive details is seen in *Matuta* which, like the Raninidæ, is at once a swimming and a burrowing crab. It is presumed that the lanceolate form of dactylus is more useful as a pick, the kukri-shaped dactylus as a shovel, but the latter may be serviceable in swimming, just as a shovel may on emergency be used as a paddle. In *Zanclifer* the dactyli of all the pereopods are narrow and sickle-shaped; they seem ill adapted for swimming but effective instruments for digging. The criterion for deciding whether a limb is utilised for swimming or for digging consists in the length and mobility of its joints. The short strong limbs of *Ranina* showing restricted mobility at the joints are clearly fossorial and ill adapted for natation: the somewhat longer and more mobile limbs of *Notopus* and *Notopoides* are, however, serviceable for both purposes. In *Notosceles* (figs. 2 & 3) the dactylus of the second pereopods is sickle-shaped as in *Zanclifer*, and it may be inferred that this pair of limbs is specialised for digging, but it can hardly be doubted that the broad kukri-shaped dactylus of the third pair, hinged fanwise to the outer angle of the transversely elongated propodus and provided with a marginal fringe of long setæ, is specially adapted for swimming. The reduced fourth pereopods of this genus, with their small flat elliptical dactyli, can hardly be of any value in digging and are rather suggestive of steering paddles.

Though *Notosceles* is in several respects intermediate between *Notopoides* and *Raninoides*, the last-named genus (figs. 5 & 6) has many distinctive features, most of which may be explained as adaptations to a swimming habit. The carapace is elongated, and its flanks taper so evenly posteriorly that it may fairly be described as boat-shaped. The first abdominal tergum is notably narrower than the posterior margin of the carapace, and the whole abdomen is narrow and more distinctly flexed under the thorax than is usual in Raninidæ. On the ventral surface there is a broad and long flat plastron in the formation of which the eleventh and twelfth sterna take an even larger share than the tenth (fig. 6). The twelfth sternum is of considerable length antero-posteriorly and is also broad and nearly flat. The articular cavities of the second pair of pereopods are placed at its hinder border and face backwards. The thirteenth sternum being very short, the articular cavities of the third pereopods are close to those of the second, and the two pairs of limbs, whilst closely contiguous to one another, are separated by the whole length of the twelfth sternum from the first pereopods. The last pair of pereopods are so reduced and slender that they are usually described as fili-form ; they terminate in minute pointed dactyli. The reduction of the last pair of legs and the narrowing of the base of the abdomen seems to be correlated with the suppression of the posterior branchial orifices ; at any rate, I can find no trace of these orifices in *Raninoides*. Nor could they be of much service if present, for the external water conduits which in other forms admit of a flow of filtered water to these orifices are here wanting. Though the eleventh, twelfth, and thirteenth thoracic epimera are as much exposed to the surface in *Raninoides* as in other Raninidæ, they are not concave and are scarcely overhung by the edge of the branchiostegite. The epimeron of the eleventh somite is relatively small, and so far from being concave that it is slightly convex. The epimera of the twelfth and thirteenth somites are obliquely grooved, and into these grooves the meri of the second and third pereopods, when bent forwards and pressed against the sides of the body, fit so closely that no water can pass between. The first pair of pereopods are slender, and when at rest are directed forwards, their large cordate dactyli being pressed against the bases of the chelipeds. Their function is obscure, but probably they are used for digging. The characters of the second and third pereopods are clearly shown in fig. 6. In these limbs the coxa and basis are directed backwards : the short ischium is nearly transverse to the long axis of the body : the merus is long and slender : the carpus normal, but it is to be observed that both it and the merus are scantily furnished with short hairs. The propodus and dactylus are flat and greatly expanded and the "fan-hinge" between them is a noticeable feature. A fringe of long stiff hairs is borne on the hind edge of the propodus and on the inner margin of the dactylus. The

efficiency as organs of natation of these broad blades borne at the end of slender and very mobile limbs is apparent. Evidently *Raninoides* is a strong swimmer and a poor digger, and as such stands at the end of the series opposite from *Ranina*. As the posterior branchial orifices are absent, one might expect to find special arrangements for an incurrent respiratory stream in the frontal region, but, though I have looked carefully for such, I have been quite unsuccessful. However, I will deal with this question further on.

*Lyreidus* (fig. 4) exhibits so many resemblances to *Raninoides* that one can hardly doubt that the two are closely related, yet, as I shall show, they are clearly adapted to different conditions of life. In *Lyreidus* the abdomen is narrow; its first three segments lie nearly in a straight line with the carapace, but the fourth is of peculiar shape, bears a strong median dorsal spine, and constitutes as it were the knuckle of a sharp ventral flexure. The sixth abdominal segment is long and narrow: its posterior angles are produced into small aliform processes which at first sight might be mistaken for vestigial uropods, but they are only processes of the tergum having on their ventral surfaces small concavities which, when the abdomen is flexed to its fullest extent, engage with small knobs on the two pterygoid processes extending backwards from the twelfth sternum. No such apparatus for locking the flexed abdomen to the sternum is seen in any other Raninid. The last pair of pereopods are so slender that, like those of *Raninoides*, they may be described as filiform: they terminate in small flattened elliptical dactyli. Correlated with the reduction of the abdomen and of the last pair of pereopods is the absence of posterior branchial orifices. I have studied this point carefully and am certain that these orifices are non-existent in *L. tridentatus*, nor could I find any trace of them in the large specimen of *L. channeri* in the Natural History Museum. As there are no posterior respiratory orifices the water conduits of the flanks are, as might be expected, absent. The epimera of the posterior thoracic somites are nearly flat and the edge of the branchioségite is but slightly prominent and bare of setæ. In the frontal and oral regions there are also many points of resemblance. Though the "front" is truncated and scarcely narrower than the broadest part of the carapace in *Raninoides*, the distance between the extra-orbital spines and the lateral spines shows that this region has undergone elongation. Further examination shows that it is the antennary somite that has been lengthened, for the antennary sternum, which has more or less the shape of an equilateral triangle in *Notopus* and *Notosceles*, is an isosceles triangle in *Raninoides*. In *Lyreidus* the elongation of the antennary somite is carried to an extreme, and the front being narrowed, the fore part of the carapace is produced into the snout characteristic of the genus, the lateral spines being situated far behind the orbits. As I shall show further on, the details of the

antennules and antennæ are extraordinarily similar in *Raninoides* and *Lyreidus* (figs. 36-39) ; so also are details in the first and second and even in the third maxillipeds. In all these things the relationship seems very close, but in other respects the two forms are divergent. In *Lyreidus* the eleventh sternum is large but narrowed between the articulations of the first pereopods and produced backwards into two small pterygoid processes which form the sides of a hollow in which the last segment of the abdomen can be lodged, as described above. Owing to the presence of these pterygoid processes the twelfth sternum appears to be deeply fitted, but it is really short, narrow, and flat, in this differing much from *Raninoides*. The thirteenth sternum being also short the coxæ of the first three pairs of pereopods are close together, and in this respect *Lyreidus* resembles *Notopus* rather than *Notopoides*, *Notosceles*, or *Raninoides*. In the first and second pereopods of *Lyreidus* the ischimerus is long, slender, and scantily fringed with hairs ; the carpus rather short ; the propodus nearly twice as long as it is broad ; the dactylus elongate and almost styliiform, with a strong external ridge. In the third pereopods the propodus is about as broad as it is long and the dactylus cultriform. These are clearly digging and walking legs, and one may conclude that the descendants of a form in which reduction of the abdomen and last pair of legs led to the suppression of the posterior branchial orifices, diverged as they adopted a more exclusively swimming habit into *Raninoides*, as they became more exclusively burrowers into *Lyreidus*. *Lyreidus* must bury itself deeply, with the tip of its narrow elongated snout just breaking the surface of the sand. Having no posterior branchial orifices it must be dependent on an inhalant current setting in somewhere in the region of the snout. One would expect some specialised inhalant apparatus, but there is very little evidence of such. Indeed, it is a singular thing that *Ranina*, *Notopus*, and *Notosceles*, all of which have well-developed posterior branchial orifices, have in addition much more specialised orbital and antennary arrangements for directing the flow of an incurrent respiratory stream than have *Raninoides* and *Lyreidus*, in which posterior respiratory orifices are absent. In *Notosceles* the antennary structure is not very different from that of *Ranina*. The flagellum is longer (figs. 41 & 41a), but the thick shortened segments of the peduncle, the flabellate shape of the fourth joint with its fringe of plumose hairs, the greatly developed crest of the third joint also fringed with hairs, are very similar. So also is the flabellate shape of the basal joint of the antennules. Fig. 57 is a frontal view of the "face" of *Notosceles* showing the antennæ as nearly as I can draw them in their natural position. In the centre, below the rostrum, is the narrow exhalant passage bounded by the basal joints of the antennules. The orbits are closed below by the crests of third segments of the antennary peduncles, and the spaces below are filled in by the proximal segments of the antennæ which in

their turn are overlapped by the broad anterior margins of the meri of the third maxillipeds. The left antenna is closed nearly as far as it will go against the antennule, and this is the more normal position: that of the right side (the spectator's left) has been pulled outwards to show the passage between the third and fourth joints of the antennary peduncle and the basal joint of the antennules. Through this passage water can pass from the orbits to the inhalant chamber covered in below by the meri of the third maxillipeds. The arrangements are very much the same as in *Ranina* though somewhat less highly specialised. In *Raninoides* (figs. 36 & 37) and *Lyreidus* (figs. 38 & 39) the basal joints of both antennules and antennæ are longer and more slender, and to that extent more primitive than in *Notosceles* and *Ranina*. In the antennules the admedian surfaces of the basal joints of the antennules are expanded and somewhat concave, so that when opposed they form a conduit for the exhalant current. The third segment of the antennary peduncle is long; a good deal longer in *Lyreidus* than in *Raninoides*. The crest is prominent but narrow, and extends nearly as far forward as the end of the fourth segment. The proportions differ slightly in the two species, but the general character is the same. The nature and distribution of the hairy fringes are clearly shown in the drawings. The relative positions of the antennules and antennæ are shown in fig. 58 for *Raninoides*: they are hardly different in *Lyreidus*. It will be observed that the "spout" of the antennary sternum is produced to open well forward between the basal joints of the antennules: it hardly extends as far forward in *Lyreidus*. In both genera, but to a greater extent in *Lyreidus* than in *Raninoides*, the third peduncular segment of the antenna is overlapped by the tip of the elongated merus of the third maxillipeds, and the portion not overlapped is covered by a tuft of long hairs projecting forward from the tip of the merus. The inner faces of the third peduncular segments of the antennæ and their crests are so shaped that when bent inwards they fit very exactly to the outer surfaces of the basal joints of the antennules, and when in this position completely bar the passage of water from the orbits to the inhalant chamber above the third maxillipeds. But when the antennæ diverge slightly outwards a clear passage is left between the antennules and the antennæ, and the intrusion of sand is guarded against by the overlapping bristles of both. Through this passage, I think, the inhalant current must pass when the scaphognathite is working normally, and through it the excurrent stream must flow when the action of the scaphognathite is reversed. But the subject is very obscure, and I am by no means content with this explanation. I give it for what it is worth in the hope that some favourably placed naturalist may read it, find fault with it, and straightway proceed to make observations and experiments on the living animals. The results cannot fail to be of interest. I feel certain only of this, that there is an inhalant current between the third and

the second and first maxillipeds. It is to direct this current under the edge of the mouth frame into the branchial chamber that the exopod of the second maxilliped is elongated and modified by being channelled along its ventral surface. The modification is carried furthest in *Notosceles* (fig. 44) and *Ranina* (fig. 42), two forms in which the accessory antennary modifications are highly developed, and in these the exopod has lost its flagellum. But in *Notopus*, in which genus the antennæ are most highly specialised for respiratory purposes, the exopod in question (fig. 32) retains a large flagellum, and the flagellum is present but small in *Lyreidus* (fig. 52) and *Raninoides* (fig. 49). This may seem a trivial character, but it gains importance when comparison is made with the same appendage in the Leucosiidæ. In *Philyra lævis* for example (fig. 54) the exopod of the second maxilliped is of simple shape, shorter than the endopod and convex ventrally. In this species, as in all the Leucosiidæ, there is a definite exostegal canal covered in below by the exopod of the maxilliped: the second maxilliped, therefore, does not lie in the course of the incurrent stream and is not modified. I have already (p. 54) called attention to the difference between the first maxillipeds of the Raninidæ and those of other Oxystomatous crabs. Indeed, as I have already indicated when dealing with the endophragmal skeleton, the anterior thoracic sterna, and other structures, the Leucosiidæ differ in a hundred ways from the Raninidæ, and I regard the comparison with *Lyreidus* as wholly illusory. The exostegal canal of the Leucosiidæ is most probably derived from the shallow groove in the pterygostome occupying the same position in *Cyclodorippe*. It would be interesting and not wholly irrelevant to attempt to trace out the various lines of descent in the families of Oxystomata other than the Raninidæ, and I have collected much evidence on this subject based on a study of the endophragmal skeleton and other anatomical features not taken into account by M. Edwards and Bouvier. But it would almost double the length of this memoir if I were to make the attempt. I have already written enough, and have, I hope, proved my main thesis that the Raninidæ cannot have descended, by way of the Dorippidæ and the Dromiacea, from the Macrura. They have originated independently from the last named, and must therefore be separated from other Oxystomes as a separate tribe Gymnopleura. I have endeavoured to show that the numerous brachyuran features exhibited by this tribe must be explained by their having adopted the same habits as other crabs, and that such modifications as the reduction of the abdomen; the loss of the uropods; the adherence of the branchiostegite to the thoracic epimera (exhibited, however, in a quite peculiar manner in the Gymnopleura); the expansion of the ischium and merus of the third maxillipeds; the broadening of the front, with which is correlated the formation of orbital cavities and the reduction of the rostrum; the great development of the muscle-cavities of the thorax,—are all characters of high survival value in decapods which have acquired the habit

of burrowing in the sand for protection and concealment. A decapod crustacean which habitually passes a large part of its existence buried in the sand, must undergo a considerable modification of its respiratory arrangements, and I have attempted to give an intelligible account of these modifications in the various members of the *Gymnopleura*. In the end they lead, as is natural enough, to the suppression of the inhalant current at the hind end of the thorax and to the substitution of inhalant currents in the antennary region. I have said, in the earlier part of this memoir, that the *Gymnopleura* are crabs *by definition*. They retain so many Macruran features that they cannot be said to be crabs by ancestry, and there is one small Macruran feature which I have omitted to mention before because I only recognised it when the greater part of this paper was written. The statocyst, usually closed in the *Brachyura*, is open in the *Gymnopleura*. (Certainly so in *Ranina*, *Notosceles*, and *Lyreidus*, but I have not been able to satisfy myself of the existence of the aperture in all the species examined because the antennules are very small and I have not been able to cut sections. The position of the aperture of the statocyst is clearly shown in fig. 34 for *Ranina*.)

I must conclude with a description and definition of the new genus and species *Notosceles Chimonis*.

There can be little doubt that *Raninoides serratifrons* of Henderson (36) belongs to the genus *Notosceles* and not to *Raninoides*, but his species, from Ceylon, is different to mine. He mentions another example of *serratifrons* from Holothuria Bank, N.W. Australia, as being in the collections of the British Museum of Natural History, but I was unable to find it there. There are considerable differences between *Notosceles* and *Raninoides*, many of which have been referred to in the course of this paper.

#### NOTOSCELES, nov. gen.

Carapace ovate, convex from side to side, minutely punctate or smooth for the most part but granular towards the frontal region; fronto-orbital border little more than half as wide as the broadest part of the carapace; the frontal region marked off by a slight transverse ridge joining the bases of the extra-orbital spines; the rostrum pointed, fairly prominent with two flat lateral and basal teeth. Ocular peduncles rather short, their terminal joints inflated, their corneæ of moderate size. Antennal peduncle short and broad, the flagellum small. Merus of the third maxilliped little more than half as long as the ischium. The second and third sternal elements of the sternal shield (sterna xi & xii) broad and convex in front, but narrowed posteriorly so that the bases of the first as well as the second pereopods are approximated to the middle line. Last pair of pereopods reduced in size, situated above and in front of the penultimate pair, their dactyli small, oval,



and flattened. First abdominal tergum not much narrower than the posterior margin of the carapace, about equal in breadth to the second tergum, the remaining terga progressively narrower; the telson small and triangular.

*NOTOSCELES CHIMMONIS*, n. sp. (Pl. 4. figs. 2 & 3.)

Carapace minutely punctate to smooth over the greater part of its surface, but granular towards the frontal region: proportion of length to breadth of carapace about 5 : 3. The frontal region is marked off by a distinct transverse ridge joining the bases of the extra-orbital spines. The median frontal region is fairly broad and produced anteriorly into a median pointed rostral spine at either side of the base of which is a triangular flattened and somewhat upturned spine, the margins of all three spines minutely serrated. On either side a fissure separates the median frontal projection from a short triangular tooth or spine, and outside the latter is a prominent incurved extra-orbital spine. A single lateral spine occurs on either side of the carapace a short distance behind the extra-orbital spine, and nearly of the same size as the latter. On the upper surface a slight carina runs from the median rostral spine to the transverse granular ridge separating the fronto-orbital region from the rest of the carapace. In the chelipeds the anterior edge of the ischium is serrated; the merus largely dilated externally at its base; the carpus granular above and without a distal spine; the propodus bears two subequal spines on its lower margin, and on its upper surface are two parallel ridges separated by a narrow groove; the immobile claw bears four denticles on its inner margin. In the third maxillipeds the relative length of the merus to the ischium is as 6 : 10; the lower surface of the merus is granular and hairy. The pterygostomial regions are hairy. In the sternal region the chelipedal sternum is of the shape characteristic of the Raninidæ, the following sternal element flat, broad in front and narrow posteriorly; the third element of the sternal plastron triangular, convex, the apex of the triangle anterior. The articular cavities of the first and second pereopods approximated to the middle line. The first abdominal tergum is flat and quadrangular, not much narrower than the posterior margin of the carapace; the second abdominal tergum is nearly equal to it in width; the remaining abdominal terga narrow rapidly and the telson is small and subtriangular in shape.

Two specimens from the Sulu Sea, both males. Length of the larger specimen with the abdomen fully extended 28 mm.: length of carapace 20 mm.: greatest width of carapace 13 mm.

The species is named after Captain Chimmo, R.N., of H.M.S. 'Nassau,' whose collections from the Sulu Sea were presented to the Oxford University Museum in 1872.

I am of the opinion that *Raninoides serratifrons*, Henderson (36) should

be placed in the genus *Notosceles*, which differs from *Raninoides* in the proportions of the carapace, the shape of the rostrum, the lesser width of the fronto-orbital region, the larger corneæ of the eyes, the proportions of the joints of the antennal peduncles, and in other characters, but especially in the relatively much greater width of the base of the abdomen, and the proportions and shape of the sternal shield.

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## EXPLANATION OF PLATES 4-7.

### LETTERING.

*A*<sub>1</sub>. Antennules. *A*<sub>2</sub>. Antennæ. *abr.* arthrobranch. *ad.* apodeme. *aph.* arthro-phragm. *at.* antennal respiratory tube. *bst.* branchiostegite. *cr.* crest of antenna. *edpl.* endopleurite. *edst.* endosternite. *en.p.* endopodite. *Ep.* Epimeron. *ep.ad.* epimeral apodeme. *ep.* epaulette of the tenth sternum. *ex.* excretory pore. *exp.* exopodite. *g.* ganglia of nerve chain. *lb.* labrum. *mbr.* mastigobran. *md.* mandible. *oc.* ocular peduncle. *oc.t.* tergum of the ocular segment. *œ.* œsophagus. *P.* Persiopoda. *pbr.* podo-branch. *ppt.* pterygostome. *plbr.* pleurobranch. *R.* Rostrum. *sbr.* rudimentary setobran. of the third maxilliped. *scy.* aperture of statocyst. *spd.* strophidium. *spng.* strophingium. *st.a.* sternal artery. *st.c.* sternal canal.

The roman numerals refer to segmental structures, sterna, epimera, ganglia, etc. Intersegmental structures are indicated thus ix/x.

## PLATE 4.

- Fig. 1. Ventral view of *Notopus dorsipes*, de Haan. The chelipeds have been turned outwards and the pereopods are extended to show their structure as far as possible.
- Fig. 2. Dorsal view of *Notosceles chimmonis*, nov. gen. et sp. The chelipeds and pereopods have been extended as in fig. 1.
- Fig. 3. Ventral view of *Notosceles chimmonis*.
- Fig. 4. Ventral view of *Lyreidus tridentatus*, de Haan. Note the elongated digging dactyli of the first and second pereopods.
- Fig. 5. Dorsal view of *Raninoides personatus*, White MS., Henderson. The first and third pereopods of the left side are missing.
- Fig. 6. Ventral view of the same specimen as fig. 5. Note the large size of the sternal plastron, due to the great enlargement of sternum xii and the adaptation of the second and third pereopods for swimming.
- Fig. 7. Left side view of *Notopus dorsipes*. The first three pairs of pereopods have been pulled downwards to show the large extent of epimera xi and xii left uncovered by the edge of the branchiostegite.
- Fig. 8. Central nervous system of *Ranina dentata*. i. ocular, ii. antennular, iii. antennary nerves; iv. mandibular nerves; v-ix. nerves to maxillæ and maxillipeds issuing from the subœsophageal ganglion; x. ganglion of cheliped; xi-xiv. ganglia of the four posterior thoracic segments; xv-xx. ganglia of the abbreviated abdominal nerve chain. *st.a.* aperture for passage of the sternal artery.
- Fig. 9. Right half of the endophragmal skeleton of *Ranina dentata* as seen from within after division into two halves by a sagittal cut. The more anterior thoracic somites are omitted. The thoracic portion of the central nervous system is shown *in situ*. Note the great depth of the sagittal apodemes of sterna xii, xiii, and xiv. *g.* 11 *g.* 14, the four posterior thoracic ganglia.
- Fig. 10. Central nervous system of *Lyreidus tridentatus*. Lettering as in fig. 8.
- Fig. 11. A drawing from the left side of the eleventh and twelfth segments of the common lobster to show the relations of the endophragmal to the exoskeleton. xi and xii. sterna of the eleventh and twelfth segments. The preparation has been slightly tilted to the right to show the endopleurites *edpl.*, consequently the epimera *Ep.* xi and *Ep.* xii are foreshortened.
- Fig. 12. A left side view of the thoracic skeleton of *Dromia vulgaris*. The ventro-lateral projections of the sterna have been omitted, and the preparation is slightly tilted over to the right. xi-xiv. the four posterior thoracic sterna.

## PLATE 5.

- Fig. 13. A posterior view of the thoracic skeleton of the common lobster, showing the large size of the penultimate and the structure of the last thoracic sternum.
- Fig. 14. A posterior view of the thoracic skeleton of *Ranina dentata*, illustrating the shape of the last three thoracic sterna and the formation of the sella turcica posterior. *sg.a.* sagittal apodemes.
- Fig. 15. A similar view of the thoracic skeleton of *Dromia vulgaris*. In the absence of sagittal apodemes in the posterior thoracic sterna the arthrophragms xiv/xv do not meet in the middle line, and there is no sella turcica.
- Fig. 16. The endophragmal skeleton of *Notopus dorsipes* as seen from above after removal of the upper parts of the epimera. 6, 7, 8, the articular cavities of the second maxilla and first and second maxillipeds. The endosternites *edst.* and endopleurites *edpl.* are clearly shown.

- Fig. 17. Thoracic skeleton of *Notopus dorsipes* seen from the left side, illustrating the great depth of the epimera and the oblique raised ridge on the 11th, 12th, and 13th epimera, against which the lower margin of the branchiostegite fits: ix, x, the ninth and tenth sterna; vi/vii to ix/x. intersegmental arthrophragms.
- Fig. 18. Frontal view of the thoracic skeleton of *Notopus dorsipes*. The articular socket of the second maxilla of the left side is omitted.
- Fig. 19. The antennary region of *Nephrops norvegicus*. The rostrum is cut short and the eyes, antennules, and antennæ are removed from their sockets. i. The membranous ocular sternum; ii. the antennular sternum; iii. the antennary sternum; iv. the mandibular sternum; ii/iii. the arthrophragm between the antennular and antennary fossæ. x. sclerite identified as the mandibular epimeron.
- Fig. 20. Side view of the ocular and the antennary regions of *Nephrops norvegicus*. The rostrum is cut short and the antennules and antennæ are removed. -oc.l. sclerite representing the tergum of the ocular segment; i. the sternum of the ocular segment: the epimera of this segment are membranous.
- Fig. 21. Antennary region and buccal frame of *Æthusia gracilipes*, Miers. Ep. iv. epimeron of the mandibular segment.
- Fig. 22. Antennary region and buccal frame of *Notopus dorsipes*. The appendages have been removed, with the exception of the right ocular peduncle and the left mandible. A<sub>1</sub>, A<sub>2</sub>, sockets of the antennules and antennæ; pgl. sub-antennary lobe of the pterygostome.
- Fig. 23. A similar view of the antennary region and buccal frame of *Ranina dentata*.

## PLATE 6.

- Fig. 24. A similar view of the antennary region and buccal frame of *Notosceles chimmonis*.
- Fig. 25. A similar view of the antennary region and buccal frame of *Lyreidus tridentatus*, showing the great elongation of the antennary sternum iii. pgl. paraglossæ.
- Fig. 26. Perspective sketch of the buccal frame of *Ranina dentata*, to show the hood-shaped mandibular sternum iv.
- Fig. 27. Antennary region and buccal frame of *Dromia vulgaris*. The appendages have been removed, with the exception of the right ocular peduncle.
- Figs. 28-33. *Notopus dorsipes*. Fig. 28. Right antennule: admedian aspect.
- Figs. 29 & 29 a. Right antenna, admedian and outer aspects. 1-5, segments of the peduncle.
- Fig. 30. Second maxilla with scaphognathite.
- Fig. 31. First maxilliped. Fig. 32. Second maxilliped: note the relatively large flagellum of the exopodite. Fig. 33. Third maxilliped: note the oblique line of hairs on the ischium also seen in *Ranilia*, M. Edw.
- Fig. 34, outer and Fig. 34 a, admedian views of the right antennule of *Ranina dentata*. Note the external opening of the statocyst, scy.
- Fig. 35, outer and Fig. 35 a, admedian views of the right antenna of *Ranina dentata*. 1-5, segments of peduncle.
- Fig. 36. Outer aspect of the right antennule of *Raninoides personatus*. Note the infolding of the cuticle to form the statocyst, and the external aperture of the latter at scy.
- Fig. 37. Admedian view of the right antenna of *Raninoides personatus*. In this genus and in *Lyreidus* the two basal segments of the peduncle are indistinguishably fused together.
- Fig. 38. Admedian view of right antennule of *Lyreidus tridentatus*.
- Fig. 39. Admedian view of right antenna of *Lyreidus tridentatus*.
- Fig. 40. Admedian view of right antennule of *Notosceles chimmonis*.
- Fig. 41, outer and Fig. 41 a, admedian views of the right antenna of *Notosceles chimmonis*.
- Fig. 43. *Notosceles chimmonis*. Third maxilliped.

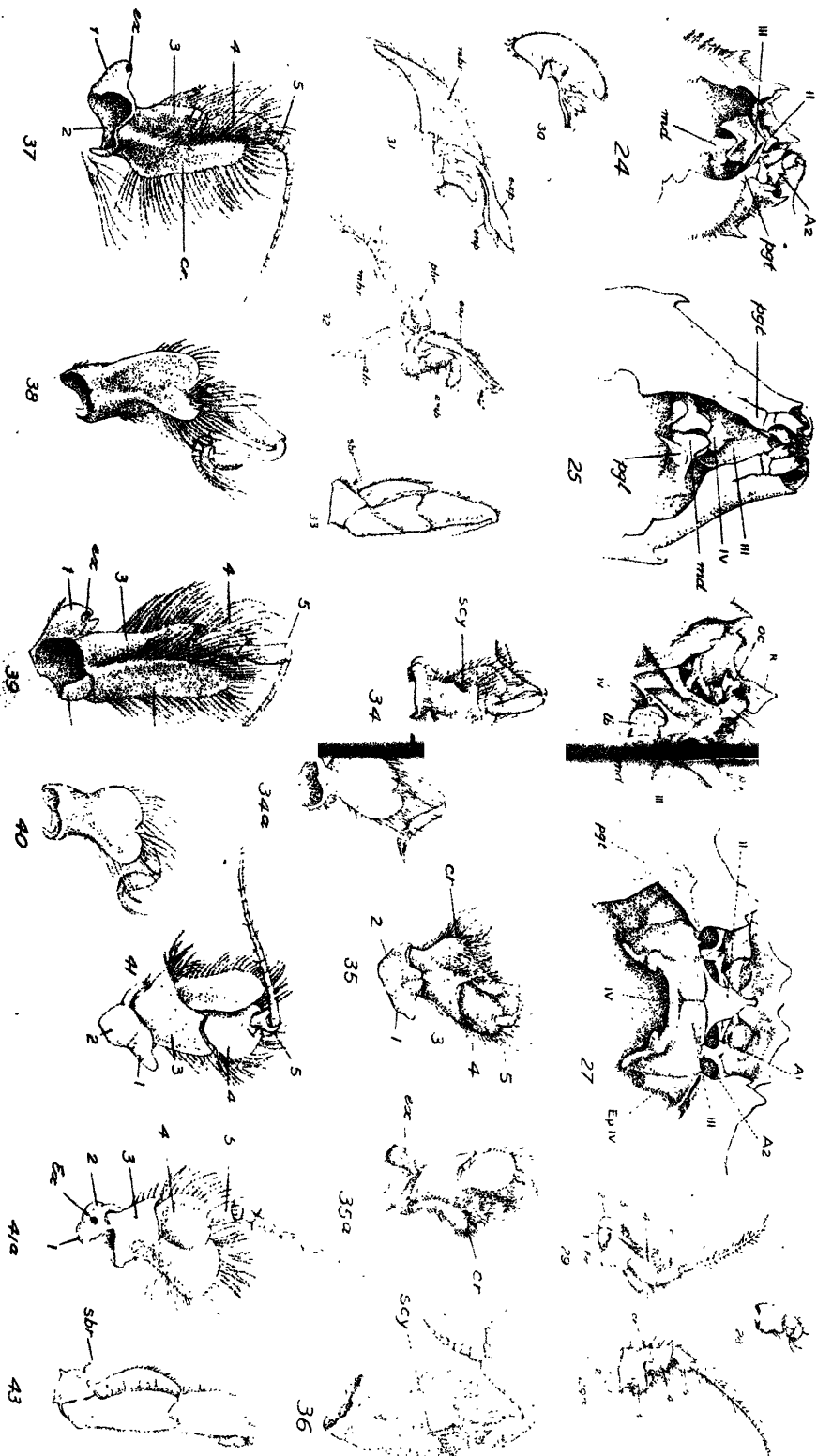


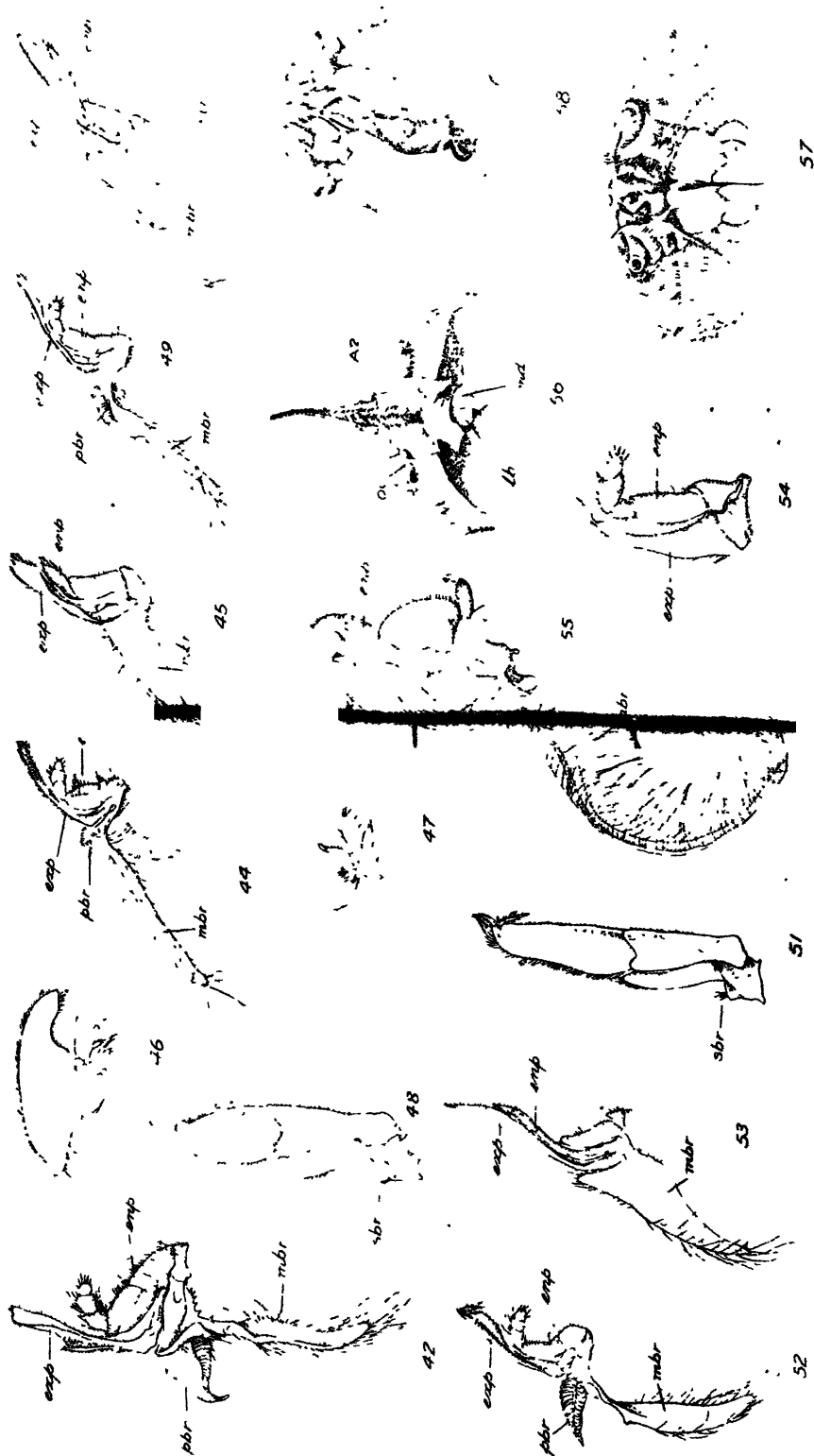














## PLATE 7.

- Fig. 42. Right second maxilliped of *Ranina dentata*. The exopodite is deeply grooved on its surface and has no flagellum.
- Figs. 44-47. *Notosceles chimmonis*. Fig. 44. Second maxilliped, the exopodite of which, like that of *Ranina*, is deeply grooved on the ventral surface and bears no flagellum. Fig. 45. First maxilliped. Fig. 46. Second maxilla with scaphognathite. Fig. 47. First maxilliped.
- Figs. 48-50. *Raninoides personatus*. Fig. 48. Third maxilliped. Fig. 49. Second maxilliped, the exopodite of which bears a minute flagellum. Fig. 50. First maxilliped.
- Figs. 51-53. *Lyreidus tridentatus*. Fig. 51. Third maxilliped. Fig. 52. Second maxilliped, the exopodite of which bears a minute flagellum. Fig. 53. First maxilliped, the exopodite of which is elongated in correlation to the elongation of the antennary sternum.
- Fig. 54. Second maxilliped of *Philyra levis*. The podobranch and mastigobranch are wanting; the exopodite is not grooved on the ventral surface and bears a short flagellum.
- Fig. 55. First maxilliped of *Philyra levis*. The mastigobranch is of great length and the exopodite is of normal shape and bears a flagellum. These appendages of *Philyra* should be compared with the corresponding appendages of the several genera of Raninidæ.
- Fig. 56. *Notopus dorsipes*: ventral view of the antennary region to show the relation of the respiratory tube to the antennary sternum. The pterygostomial portions of the carapace have been cut away.
- Fig. 57. Frontal view of *Notosceles chimmonis* to show the antennæ in their natural position and their relation to the orbits. The right antenna has been pulled slightly outwards to expose the antennules.
- Fig. 58. Ventral view of the anterior part of thorax and head of *Raninoides personatus*. The right third maxilliped has been removed and the left displaced from the middle line to expose the mouth frame and to show the elongated exopodites and endopodites of the first maxillipeds forming the floor of the spout-shaped antennary sternum. The latter extends well forward between the basal joints of the antennules.



The Theory of Recapitulation: A Critical Re-statement of the Biogenetic Law. By WALTER GARSTANG, M.A., D.Sc.(Oxon), Professor of Zoology in the University of Leeds. (Communicated by Prof. W. BATESON, F.R.S., F.L.S.)

(With a Text-figure.)

[Read 2nd June, 1921.]

More than half a century has passed since Haeckel propounded his "fundamental Biogenetic Law" (1866). It played a great part in the campaign for the recognition of Evolution, has inspired and still inspires much good work in Palæontology, but, as a working hypothesis in Embryology, is admitted to have evoked little but controversy and confusion. This history alone renders it probable that the law is a mixture of sound and questionable elements, but the two have never been satisfactorily disentangled. The late Dr. C. H. Hurst (1893), Adam Sedgwick (1894 & 1909 (*a*)), and Geoffrey Smith (1911), Oscar Hertwig (1898 & 1896), and Morgan (1908), among others\*, have criticised particular aspects of it, but no one has presented a complete theoretical scheme capable of replacing Haeckel's as an explanation of the relations between ontogeny and phylogeny. Lately MacBride (1914 & 1917), from the embryological side, and Bather (1920), from the standpoint of palæontology, have revived the full Haeckelian doctrine; and the former has even considerably extended it, though neither, so far as I can see, has refuted, or even appreciated, the force of the criticisms made by their predecessors. As it is not to the credit of science that Zoology should harbour a "law" which, like a creed, may be accepted or rejected at pleasure, and as I believe the basis of this law is demonstrably unsound, I venture to make a renewed attempt to define the points at issue. The most satisfactory way of doing this appears to be to re-state, in accord with modern knowledge, the theoretical relations of ontogeny to phylogeny, and then to subject the alternative theories to verification by test-cases. As the old law was essentially morphological, I exclude from present consideration all bionomical and ætiological questions not directly involved.

1. The two aspects of Haeckel's doctrine—the statement of fact and the theory of causation—were summed up by himself in the phrases: "Ontogenesis is the recapitulation of Phylogenesis" and "Phylogenesis is the mechanical cause of Ontogenesis." In these now familiar terms the new

\* Bateson's criticism of the law of von Baer, though not specially referring to Haeckel's modification of it, should be included here (1894, pp. 8-10).

conception of evolution was wedded, fifty years ago, to current ideas of ancestry, heredity, and development: Ancestors created, heredity transmitted, and development repeated the order of creation.

2. To Haeckel, phylogenesis meant "the chain of manifold animal forms which represent the ancestry" of an organism, *i. e.* the phyletic line of succession of adults. Ontogenesis was, and is, the succession of form-changes between zygote and adult of the same organism. The ontogenetic sequence was regarded as resembling, and actually caused by, the phyletic sequence of adults, which had preceded it.

3. But Haeckel overlooked the other evolutionary sequence, the phyletic line of succession of zygotes, running more or less parallel with the adult sequence, step by step, though steadily diverging. Every elaboration of adult form, even of its degree of pliability under environmental influence (for there are great differences among animals, as among plants, in this respect), was preceded by a corresponding elaboration of zygotic structure\*, nuclear or cytoplasmic or both, determining, under suitable conditions, the form and character of the ontogenetic changes and their result. Through the whole course of Evolution, every adult Metazoan has been the climax of a separate ontogeny or life-cycle, which has always intervened between adult and adult in that succession of forms which Haeckel terms "Phylogenesis." The real Phylogeny of Metazoa has never been a direct succession of adult forms, but a succession of ontogenies or life-cycles.

4. This was so from the very beginning, when zygote and adult were indistinguishable in form as ancestral Flagellate Protozoa. Zygosis must have been followed, then as now, by successive cell-divisions, corresponding to the cell-divisions of Metazoan ontogeny, though they led to no single multicellular adult. A stage further on, the corresponding cell-divisions gave rise to adherent colonies, fixed or free, arborescent or epithelial, each type established by its own ontogeny. The very first, most ancestral Metazoan of all—at whatever grade of evolution the dividing line may be drawn—must be admitted to have been built up by a full ontogeny from unicellular zygote to multicellular adult, so that, in the first, as in the latest Metazoan, ontogeny came first, leaving the first adult Metazoan as its original achievement. The next generation, through a new ontogeny, produced a second adult, and so on. In a word, Haeckel's causes and effects must be inverted. Phylogeny (in Haeckel's sense) is the product, the "record"—not the precedent cause—of successive ontogenies; and neither the first, nor the second, of Haeckel's phrases can any longer express the basis of true biogenetic law. Ontogeny does not recapitulate Phylogeny: it creates it.

\* Cf. Hertwig (1906, i. p. 56): "Die Eizelle z. B. eines jetzt lebenden Säugetieres ist kein einfaches und indifferentes, bestimmungsloses Gebilde . . . sondern . . . das ausserordentlich komplizierte Endprodukt eines sehr langen, historischen Entwicklungsprozesses."



5. Does this involve, then, the loss of the doctrine of Recapitulation? To which question I reply, first, with Goethe, "Was fruchtbar ist, allein ist

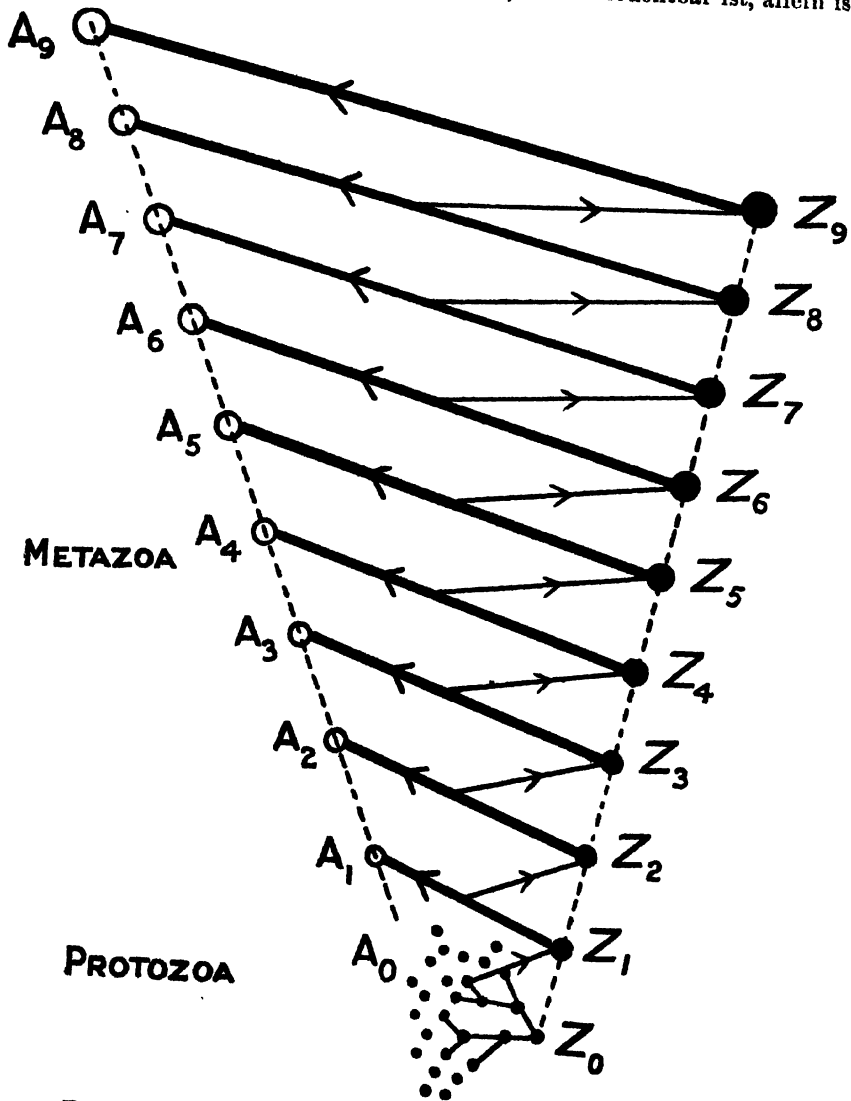


FIG. 1.—Diagram of the Relations between Ontogeny and Phylogeny.  
 $A_0$ - $A_9$  ..... the Phyletic succession of Adults.  
 $Z_0$ - $Z_9$  ..... do. do. do. do. Zygotes.  
 $Z_1$ - $A_1$  } ..... do. do. do. do. Ontogenies.  
 $Z_2$ - $A_2$  }  
 &c. •

wahr," and, secondly, as Balfour wrote on another matter: "If the above position be admitted, it is not permissible to shirk the conclusions which seem

necessarily to follow, however great the difficulties may be which are involved in their acceptance" (1885, ii. p. 32). But the "parallelism" of ontogenetic and phyletic sequences, which was incorporated by Haeckel in his "law," was noticed by many a "good physiologist" before him (*cf.* Meckel, Von Baer, L. Agassiz, &c.), and cannot disappear with his interpretation of it. Perhaps now we shall see its true extent and meaning more clearly. Ontogeny proceeds through successive *grades of differentiation* by which layers, tissues, organs, and parts together with ordinal, family, generic, and specific characters, are more or less successively established. As differentiation increases, the combination of layers, tissues, organs, and parts exhibited at successive stages resembles more or less distinctively the combinations characteristic of successive *grades of evolution* represented in our schemes of phyletic classification. To that limited extent the ontogeny of a given animal is an epitome of its phylogeny, and may be said, in the true sense of the word, to recapitulate phylogeny, *i.e.* to sum it up, recall the main phases of it. This is the parallelism observed by Meckel, Von Baer, and many others, expressed in evolutionary terms. It exists and is undeniable.

6. This parallelism exists because phylogeny is itself the creation of successive ontogenies, and ontogenies of necessity run parallel with one another from zygote to adult. For ontogeny is the expression of zygotic power, the function of zygotic structure; and zygotic change involves no radical departure from the routine of ontogenetic method. One ontogeny is, in this sense, a modification of its predecessor. The ontogeny which first established the Cœlenterate grade was the basis of a later ontogeny which established the Cœlomate grade. The life-cycle was extended accordingly, but never by the simple addition of a substantial unit or stage, distinctively Cœlomate, to the final adult stage of a Cœlenterate ontogeny. A house is not a cottage with an extra storey on the top. A house represents a higher grade in the evolution of a residence, but the whole building is altered—foundations, timbers, and roof—even if the bricks are the same. You may begin by building a cottage a little larger than its predecessor, cutting off an entrance passage from the parlour, and adding a back kitchen; but when your ambition rises to an entrance hall, three reception rooms, two staircases, and so on, you are forced to a mutation in your building plans which affects operations from the start. The ontogeny of a Cœlenterate adds, in a certain sense, on a simple diploblastic base, certain effective, workaday, adult features by which it copes with the conditions of its life; but the replacement of these effective characters by others suited to the more adventurous career of a Cœlomate (*e.g.* development of prehensile mouth instead of tentacles) involves their disappearance altogether; and there remains of Cœlenterate organisation only that diploblastic residuum of differentiation out of which the Cœlomate may be economically and directly built up. Nor is the end of

the life-cycle alone effected. The Cœlenterate had a larva fitted both to distribute it and to build it up. It must be changed so as to perform this double function for a quite different creature, probably of very different size, habits, and requirements. And then the changes at the larval end must be fitted and co-ordinated with the changes at the adult end, so that every phase of the life-cycle is modified in some way or other. Yet it is only this much-pruned Cœlenterate sequence that survives as building material out of which a specifically Annelid ontogeny may give rise to a Crustacean, and so on. Inevitably the Cœlenterate sequence in the Crustacean's ontogeny is reduced to the simplest terms, and is as far from "mirroring" any functional Cœlenterate type, or the original mode of its formation, as possible. Nevertheless, the grades persist as stepping-stones from zygote to adult; and, having been successively pruned of unessentials as they ceased in turn to furnish directly the equipment of the adult stage, they have become very constant features of the ontogeny in a long line of evolutionary progress. For there is an irreducible minimum beyond which even ontogeny cannot abbreviate. The zygote is always unicellular, the larva multicellular and fitted for swimming, and the adult a multilaminar complex of interdependent parts; and even the Ctenophore, with its elaborate præ-organisation of the zygote, cannot escape the rule that  $8=4 \times 2$ . Ontogeny repeats the necessary successive grades of ancestral differentiation, but no ontogenetic stage is ever more than an immature adumbration of a particular adult type in the phyletic chain\*. It reproduces those successive grades, not because successive adult types have been included in it, but because each ontogeny is a modification, within limits, of its predecessor; and by those predecessors the phyletic chain of adults was organised and equipped.

7. Thus Cœlenterate, Cœlomate, Protochordate, Gnathostome, and Tetrapod are successive grades of differentiation both in the ontogeny and phylogeny of a Frog; but at none of these grades does the ontogeny recall the form and structure of a possible adult ancestor. This is obvious enough in each of the first three grades; and in the fourth, which is held to "recapitulate" the Fish, the tadpole lacks dermal skeleton (both scales and fin-rays), paired fins, and biting jaws, which the adult ancestral Fish undoubtedly possessed. The tadpole, in fact, is not a modified reproduction of an adult Fish-ancestor, but a modification of the larva which that ancestral fish undoubtedly possessed—still recognisable, in less modified form, in the larvæ of *Polypterus* and Dipnoi to-day. In other words, the life-cycle of the Frog is a modification of the life-cycle of an ancestral freshwater Fish; and adjacent terms in the old life-cycle (larva and adult) have undergone parallel and correlated modifications, as well as some independent specialisations.

\* Cf. Von Baer (1828, p. 230): "Der Embryo geht nie durch eine andere Tierform hindurch, sondern nur durch den Indifferenzzustand zwischen seiner Form und einer anderen."

8. That "recapitulation" does not require the reproduction of adult stages in the ontogeny in order to be exhibited is plainly seen in the development of many Geometrid moths. Everyone knows the Geometrid or "looper" type of caterpillar, provided with prolegs only on two of the hindmost abdominal segments (the 6th and last). This type is admittedly derived from a prototype which possessed the full Lepidopteran equipment of prolegs on segments 3 to 6, as well as the last, the prolegs on the three first segments having subsequently disappeared. But many Geometrid caterpillars possess vestiges of one or more pairs of these missing prolegs : in the March moth \* (*Erannis escularia*, Schiff.) there are traces of the last pair (South, ii. pl. 125); in the common Brimstone (*Opisthograptis crataegata* (Linn.)) and Scalloped Hazel (*Gonodontis bidentata*, Cl.), clear rudiments of the last two pairs (l. c. pl. 115); while the Orange Underwing (*Brephos parthenias* (Linn.)) has the first two pairs rudimentary and the third pair fully developed and functional (Meyrick, 1895, and South, 1908, ii. pl. 39). In the Feathered Thorn, *Colotois* (*Himera*) *pennaria* (Linn.), the single pair of vestigial prolegs arises and disappears between the 1st and 4th moults (Buckler, 1897). Now, the time has long passed when it was possible to regard these prolegs as homologues and derivatives of the true legs of some Scolopendroid ancestor. They were "cenogenetic" larval features, adaptive interpolations, modifications of the middle stages of a life-cycle which originally, in the earlier phases of Endopterygote history, exhibited larvæ lacking prolegs altogether, as in Coleoptera. Yet these examples of vestigial organs are as reminiscent of ancestral (though larval) structure as the larval foot of the oyster, the larval stalk of *Antedon*, the transitory feet of the parasitic *Portunion*, or any other of the familiar examples that are held to prove the theory of adult recapitulation. They demonstrate, as Morgan has already urged (1919), that recapitulation is merely the static aspect of inheritance, and that, in this aspect, inheritance is not primarily the reproduction of adult characters, but the reproduction of the characters of each part of the whole life-cycle—the sequential expression of the full train of zygotic potencies.

9. It may be urged that such hereditary changes in the middle phases of the life-cycle do not affect the proposition that evolutionary changes usually take place at the end; and that the case for adult recapitulation rests on the evidence for this proposition. Nevertheless, to clear up the misunderstandings of the past, it is necessary to leave no margin for ambiguity. If "recapitulation," in the special sense of partial reproduction of the past, is hereby shown to be independent of the characters of adult ancestry, that is something gained : the axe is laid at the root of the tree. For much of the glamour of the old biogenetic law is due to its appeal to such idols of the market-place as the assumption that "like begets like," and that, as adults

\* Meyrick's classification and nomenclature are followed here, but the English names have been added for convenience of reference to South's figures.

only are capable of begetting, the thing begotten is built up of successive adults. That "cenogenetic" interpolations\*, without any adult ancestral significance, are a normal feature of almost every life-cycle, is often verbally admitted, though the recapitulationist rarely realises how profoundly such interpolations may affect his phylogenetic conclusions, and how dangerously subtle become his arguments when engaged in proving that such larvæ as the Trochosphere, the Nauplius, and other distributive stages of the life-cycle are at bottom "recapitulative." I propose to deal more fully with the origin and significance of such larval forms in another communication; but, to illustrate the principle, I may add one example of the origin of an interpolation in the most progressive of sequences known to us, viz. that of Vertebrates. There is no doubt that Birds are descended from Reptiles. It is beyond question that Reptiles are hatched in a form and with a somatic organisation which is that of a miniature adult Reptile in all respects. Yet the Bird is hatched in a form and with sundry details of organisation different from those of the adult, *e.g.* its downy plumage. Now, the "typical" down-feather is an open hollow tube, splayed out at its free extremity into a ring of soft barbs (or barbules) of equal size, and I ask if such a tubular feather is to be regarded as an intermediate stage in the phyletic derivation of feathers from scales. I submit that there is not a scrap of evidence, or of probability, that any adult ancestor of Birds, along the whole route from Reptiles to Sparrows, was ever clothed in anything except scales, feathery scales, and finally contour-feathers. The chick is an interpolation in the life-cycle of Birds, and its down is a "secondary" modification of complete contour-feathers. The Duck, the Fowl, and the Pigeon represent three successive grades of differentiation in the phylogeny of Birds. Anyone who will examine under a microscope the nestling-down of these three birds in the order mentioned, will see that they exhibit successive phases in the degradation (*a*) of the primitive rachis of a contour-feather and (*b*) of the barbs of such a feather, *i.e.* that the chick stage, with its peculiarities of organisation, has been evolved, step by step, within the group of Birds alone, and is an interpolation that has no relation with, and throws no light on, the præ-Avian adult ancestry, or on the way in which scales were transformed to feathers†.

\* *E.g.* Weismann's discussion of the evolution of markings in larvæ of Sphingidæ, much of which is probably sound, though unnecessarily complicated by the assumption that primitive longitudinal markings have been "shunted back" into earlier stages of the ontogeny, instead of being simply *replaced* in the later stages by patterns more suited to increased size or special conditions of exposure (1904, pp. 177-185).

† The subsequent publication of Prof. Coscar Ewart's valuable paper on "The Nestling Feathers of the Mallard" (*P. Zool. Soc.* 1921) renders this discussion inadequate and I hope to amplify it. In the meantime I would merely remark that, on the relation of feathers to scales, the association of several feather-germs with single scales on the foot of the Owl is no disproof of my thesis, since the feathers here represent a secondary extension, like that of the scales on the head of *Ceratodus*.

10. Let us now take an equally unambiguous case of evolutionary change at the adult end of the life-cycle. There is a group of genera of Geometrid moths in which the life-cycle terminates with normal winged males and more or less wingless females (*Apocheima*, *Hybernia*, *Theria*\*, &c.). It is an adaptive change, for, unlike their congeners which hibernate as pupæ and emerge in early summer, these moths emerge in winter when the trees are leafless, and the normal method of repose is much more dangerous. The males, like both sexes of other related genera, rest by day exposed with wings outspread on tree-trunks, palings, &c. The wingless females hide in the crevices of bark. Both are active at night, the females creeping out of their crannies, and the males hunting for them up and down the woods. In the Early Moth (*T. rupicaprararia*) and Dotted Border (*H. marginaria*), which emerge in February and March, the wings of the females are half as long as the body (South, ii. pl. 120); in the Scarce Umber (*H. aurantiaria*), which emerges as early as October or November, the wings are mere stumps (*l. c.* pl. 120); while in the Mottled Umber (*H. defoliaria*) and various other species the wings are completely lacking (*l. c.* pl. 122). The wings of the males are of full size throughout (Meyrick, and South, *l. c.*). Now here is a case of evolutionary change of the adult form, and in one sex only; but, with these facts before him, and with our knowledge of the origin and breeding of similar mutations in Morgan's *Drosophila* experiments, who can assert that this abnormal adult has been added to the life-cycle of its normally-winged ancestors, and that the old adult has been "pushed back" to an earlier phase of the life-history. The wingless female is the exact counterpart of the normal male, and, though I do not know if any change has already taken place in the pupal characters of the female, it is a safe deduction from our knowledge of the pupal condition in more extreme cases to assert that the only changes likely to ensue will be in the direction of still further reducing the size of the pupal wings. The ontogeny will be influenced in the direction taken by the new adult, and without regard to the ancestral adult at all. The new adult is just a modification of the old adult. There is no addition, no "tacking on" of a new stage; no "pushing back" or "tachygenesis" of the old adult stage—merely a substitution of one adult type for another, and, sooner or later, some correlated changes in the stage which immediately precedes it. Zygotic mutations have caused the changes; natural selection has controlled the breedings of successive generations; and heredity has perpetuated the results of the selection. Certain ancestral adult characters are disappearing from the ontogeny; and the condition of a flea, ontogenetically, as well as finally, without a trace of wings at any stage, is likely to be the end result.

11. I have selected this example, not because it is representative of all evolutionary changes that manifest themselves in the final stages of ontogeny, but because of its bearings on the most recent exposition of the theory

\* Meyrick's nomenclature (1895); English names and figures in South (1908).

of recapitulation from the embryological side. I have already shown that, in its original and general sense, recapitulation is a fact which was recognised long before there were any theories to account for it. But this generalised, or Meckelian, recapitulation needs to be clearly distinguished from the specifically adult recapitulation of Haeckel and his school, who could not understand the origin of the former except on a theory of catenary ancestral inheritance, each term in the ontogeny (except the last) being moulded after the likeness of a specific adult ancestor—though, of course, condensed, abbreviated, telescoped, and secondarily modified by adaptive changes. Now, the only way that I can see of establishing this theory by purely embryological methods, is to show that the penultimate stage of the ontogeny of a given type of adult resembles the final (adult) stage of the ontogeny of some theoretically ancestral type more closely than it resembles the corresponding penultimate stage of the same, and similarly with regard to the antepenultimate stage, and so on. I cannot find that this has been done, or even attempted, in any case—certainly not in any of the cases recently selected by MacBride for discussion. Yet this is his thesis: “When we assert that a Metazoan recapitulates in its life-history the past history of the race or stock to which it belongs, we mean that the stages intervening between the egg and the adult form resemble in some of their prominent features the *adult* animals which belonged to the same stock at different epochs in the past history of the race” (1917, p. 425); and he is concerned to show both that the adult stage of the ontogeny of a new species is an addition to the ancestral ontogeny (1914, pp. 23, 650), and that the adult stage of the ancestral ontogeny is reproduced (“recapitulated”) in the ontogeny of the new species as the last larval (or “neanic”) stage (*l. c.* pp. 21, 22). But his method of establishing these points is merely to select a number of cases in which the adult deviates considerably from the normal, and to show that “the young form resembles the type of the order to which the parent belongs and not the parental type itself” (1917, p. 428). “Thus the young Hermit-Crab swims freely about in the water and has a symmetrical abdomen like that of Shrimps and Prawns” [but so have the *young* stages of these creatures!]; “the young Flatfish swims with its ventral edge down and its dorsal edge up, and has an eye on each side of the head” [but so have the young of all Teleostei!]; “the young Comatulid is fixed to the bottom by a stalk like other Crinoids [and their young too, in all probability!]; and the young American Oyster possesses a foot like that of other bivalves by which it crawls about” [and, I may-add, as the *young* of nearly all other Lamellibranchs crawl about!]. Nowhere does he show, or claim to show, that the young stages of any of these animals resemble the *adult more closely than the young stage* of typical members of their respective orders. He does not show it because he cannot. In every case that he discusses, whether the above, or the cases of the parasitic *Portunion*

and *Actheres* (1914, pp. 22, 206), the young resemble the young stages far more closely than they resemble the adult stages of their respective "normal" relatives\*. The symmetrical larva of Pleuronectids is scarcely distinguishable from many Teleostean larvæ of other families: it is distinct from any existing or fossil *adult* Teleost. It is the adult Oyster which has lost its foot, not the young Oyster which has acquired it. It is the adult *Portunion* which has lost its legs, not the young *Portunion* which has acquired them by tachy- (or any other kind of) genesis from its adult ancestors! These cases are all in the same category as the case of the wingless Moths already discussed. No new stage has been *added* to the life-cycle. One adult stage has been transformed into another, but the penultimate stages remain as before. The protagonist has missed his point, and the riposte is obvious. It was not his task to prove that Oysters were Mollusks, that Hermit-Crabs were Crustacea, or Pleuronectids Fishes. Comparative Anatomy did that long before the science of Embryology staked its claim. His province was to show that by virtue of Haeckel's Biogenetic Law he could reconstruct the prominent features of an *adult* ancestor from a developmental stage. All he has done is imperfectly to confirm Von Baer's præ-Haeckelian doctrine, that animals resemble one another more closely in their young stages than in their adult stages†. For his own illustrations show how greatly the adult may differ from the larva. He has merely shown the resemblance between the larvæ of a given class. It follows that, for all he has shown to the contrary, the "typical" or "normal" larvæ, which the Pleuronectid larva resembles, might have grown into Cod, Mackerel, or any other type of Teleost, and that the *adult* ancestors of Pleuronectids, so far from being "normal," may have carried themselves upside down like a *Remora*, or stood on their tails like Pipefishes. If no more relevant evidence than this is forthcoming, I claim that the old Biogenetic Law of adult recapitulation is dead, and that Morphology is henceforth free from a delusive and cramping hypothesis. Ontogeny is not a lengthening trail of dwarfed and outworn gerontic stages. Youth is perennially youth and not precocious age.

12. It is true that ontogeny could not exhibit its normal progressive differentiation of structure if evolution had always been of the type exhibited by these examples of metamorphic Insects, Lamellibranch Mollusks, parasitic Crustacea, and Pleuronectid Fishes. Evolution within these groups to-day partakes mostly of the nature of an adaptive radiation of the various types, whereas the general lines of ontogeny correspond rather with that kind of evolution which involves morphological and physiological progress. Although a detailed examination of any of these various advances falls

\* Note especially the absence of the 8th pair of thoracic limbs in *Epicarid*, as in all other *Isopod* larvæ.

† "Im Grunde ist also nie der Embryo einer höheren Tierform einer anderen Tierform gleich, sondern nur ihrem Embryo" (1828, p. 220).



outside the purview of the present communication, the slightest survey of Vertebrate evolution shows a series of triumphs over limiting environments of medium, temperature, space and time which has been based as much on the substitution of new for old organs as on the continuous elaboration of particular ones. When a given organ is wholly transformed in the course of evolution, it rarely shows traces in ontogeny of the original steps of its transformation (*e.g.* bony scales to fin-rays, horny scales to feathers, lobate fins to pentadactyle limbs, pentadactyle limbs to wings). The final form alone is inherited and develops directly. But when originally separate organs are ultimately united into one organ, some stages of the process of amalgamation are necessarily repeated (*e.g.* branchial arches to hyoid, vertebral elements to vertebrae, muscle-buds for paired limbs, ankylosis of limb-bones, segmental tubules of kidney, &c.). And when a new organ has arisen in intimate dependence on an old organ, the old organ may still remain necessary for the development of the new (Klæinenberg, 1886). Thus backbone replaces notochord, and bone replaces cartilage in present as, doubtless, in past ontogeny, for the former organ or tissue is still necessary as scaffolding for the later one: and the constant development of gill-slits in the ontogeny of terrestrial Vertebrates is but another illustration of the same phenomenon, as Sedgwick has already pointed out (1894)—for a complex double circulation that has been elaborated along channels determined by a branchial circulation cannot readily depart from the phyletic steps of its formation. It is this formative dependence of one organ, or set of organs, on another that confers on Vertebrate ontogeny its marked recapitulative character.

13. But it is equally clear that the whole succession is explicable without recourse to the theory of successive adult incorporations, and that the ontogenetic stages afford not the slightest evidence of the specially adult features of the ancestry. So far as notochord and gill-slits are concerned, they make their appearance in the earliest larval stages of every animal that presents them, including *Amphioxus* itself. Their phyletic origin is still wrapped in obscurity. The case is hardly different as regards cartilage, bone, scales, feathers, hairs, lungs, limbs, and all the other organs concerned. No example can be adduced of any of these organs *arising* in an adult stage of ontogeny. Until that evidence is produced, it is idle to claim that recapitulation which involves any of these organs is a repetition of specifically adult ancestral features. Moreover, it is impossible to overlook the fact that some of the most pregnant changes in the characteristics of the higher Vertebrates are directly or indirectly traceable to changes in the earliest stages of the ontogeny. The elaboration of the brain in Birds and Mammals, and the development of their social and æsthetic senses, are connected with the interpolation of the helpless chick, puppy, or baby stage in the ontogeny, which from the simplest beginnings has led to the development of educability and

preferential action in place of the limited range of reflex and automatic mechanisms of more primitive types. That "little twist of brain," which distinguishes one philosopher from another, is not more striking in its effects than are those trifling touches to the structure of the heart which transformed the cold-blooded Reptile and Stegocephalan into the warm-blooded Bird and Mammal respectively. Yet these are changes which, however graduated through successive generations at the outset, were not of a character to have been completed, or even initiated, in any adult stage of ontogeny. They must have been first manifested as a series of embryonic mutations, subjected continuously to selective tests of their relative physiological efficiency. Age bears the buffets of the world, but youth regenerates it.

14. It is, however, the palæontologists who are the real defenders of the Biogenetic stronghold. With them the Law is a faith that inspires to deeds, while to the embryologist it is merely a text for disputation. The difference is striking and worth defining. When the embryologist sets up his larval images and worships them as præ-Cambrian ancestors, the real ancestors cannot be produced to demonstrate his folly. But the palæontologist's aim is to trace lineages directly, and he is not satisfied until he has produced his ancestors, or at least the most substantial remnants of them. I confess that I have been tempted many times before to-day to attack a theory which has led so many of us into blind alleys, but always Hyatt's Ammonites recurred to present an unanswered, and seemingly unanswerable case for Haeckelian recapitulation. *A priori* it seems absurd that senile characters should be the beginnings of a line of evolution (Hyatt, 1897, p. 221 &c.), but the formidable array of evidence, the wide range of unfamiliar material to be studied, and, not least, our ignorance of the habits and conditions of life of this type of Mollusk, have all conspired to render these Ammonites to me a real obstacle. The following case, however, has recently impressed me with its remarkable analogies, and justifies me, I hope, in presenting a general argument without directly tackling the Ammonite problem itself, at any rate for the present.

The curious Prosobranch Gastropod *Lamellaria*, which mimics and devours Compound Ascidians, produces veliger larvæ of a unique type known as *Echinospira* (Krohn, 1853, 1857). The hyaline shell first produced is dilated so that it is far larger than its occupant—resembling in this respect the gelatinous house of an Appendicularian. It is coiled like the shell of an Ammonite, being in some species discoidal, with perfect symmetry, in others spiral, and in the related *Onchidiopsis* more simple and sac-like (Bergh, 1887). The larva can withdraw himself completely, or, with his mantle-edge clasping the mouth of the shell, he can protrude a large 4- or 6-lobed velum, and swim about with it on his excursions with wonderful grace and ease. The mouth of the shell is regularly extended at its margin, the successive additions being marked by transverse lines of growth and generally by one or two pairs of longitudinal (spiral) rows of tubercles or spines as well.

Inside this rapidly growing house (the roof of earlier whorls being periodically destroyed to make room for their successors), the larva secretes a second flatter shell (the rudiment of the adult shell) which fits his visceral hump and adheres to it, but is temporarily fixed in the cavity of the outer shell until he shifts his position, when it is carried forward—as though he were trying to improve on an Ammonite's arrangements by the device of a portable septum \*. Now, the point of the analogy is this : that the spiral rows of tubercles on the outside of the shell are variable in different species, and that in the same individual they may go through a cycle of changes exactly like the progressive changes of an Ammonite. The shell may pass through a smooth stage, a unituberculate stage (the outer row of tubercles), a dituberculate stage (with both rows developed), a spiny stage, and lastly a ribbed stage, in which cross-ribs join the tubercles of the two rows together. Unfortunately for the completeness of the analogy, *Eclinospira* does not (so far as I have yet seen) present a gerontic stage, for, being only a larva, and usually very lively and vigorous, he quits his cage before old age comes over him, and transforms himself into a torpid Ascidian-eating *Lamellaria*. I hope to publish shortly some figures of the remarkable process of metamorphosis, of which I was lucky enough to be an eye-witness last year at Plymouth, as well as some further details of the growth of the larval shell ; but for my present purpose I refer to Simroth (1885, text-fig. 5 ; Taf. xvi. figs. 1 & 2 ; xviii. figs. 1-2, 6-8), whose excellent figures sufficiently illustrate my immediate points. Meanwhile I submit (1) that the characters of the larval shells of *Lamellaria* and its allies are purely cenogenetic, with no relationship to the characters of any adult ancestors ; (2) that gradual and progressive changes in the shell of the same individual, from one type of "ornament" to another, occur regularly, and are apparently determined by the constitution, size, and vigour of the larva under the particular conditions of its existence ; and (3) that different degrees of the power of tubercle- and spine-formation characterise the larvæ under different conditions of existence.

In this case, from which all specific influence of adult ancestry is excluded, there is no escape from the conclusion that the power to perform these variously graduated operations, and the extent of that power, are essentially functions of the zygotic constitution, though there is a considerable margin for the direct influence of conditions. I conclude that, if this is so for the "cenogenetic" larvæ of *Lamellaria*, it is not likely to have been different for the "palingenetic" stages of Ammonites.

15. I return to the keynote with a direct comparison between the ontogeny and phylogeny of an animal in which the skeleton has been an important index of racial structure throughout geological time—the Crinoid *Antedon*.

\* The two shells correspond to the two layers of an ordinary Molluscan shell, dislocated from their original union. The outer or larval shell, corresponding to the prismatic layer, is formed by mantle-edge alone ; the inner or adult shell, corresponding to the nacreous layer, is formed by the visceral surface of the mantle alone.

In selecting this type from the few that fulfil the necessary conditions, I have naturally not overlooked the fact that in the two most doughty advocates of Haeckel's law in this country, we also possess two of the foremost experts in Echinoderm embryology and Crinoid palæontology respectively. If I err in my selection, or statement, of facts to be brought into prominence, they will know, I think, that it is from inadvertence and not from intention. The test of palæontology cannot, of course, be brought to bear on the origin of the stalked condition, or at present, at any rate, of the primal torsion of the internal organs of Echinodermata; but I regard it as established by the form-sequences which Bather and his colleagues have traced, that radial symmetry was imposed upon the skeleton of an original pear- or sac-shaped body by the extension of superficial food-grooves leading to the mouth from food-collecting tentacles—a view which I understand is shared by MacBride (1911, p. 248). The hypothesis that Cystoid, Blastoid, and Crinoid were successive and independent offshoots from an unknown stock that lacked a skeleton seems to me to involve the negation of precise morphological evidence.

Accepting as my basis Bather's masterly sketch (1900) of the phyletic classification of these groups, and bearing in mind his own cautions (*l. c.* p. 138), as well as the slenderness of the geological record of Permian and Triassic forms, the main outlines of the adult ancestry of *Antedon* cannot have deviated far, I think, from the following sequence (the Roman numerals in brackets refer to certain figures of special significance in Bather's work):—

(?) Præ-Cambrian.—Præ-brachiate ancestors, first Cystoid, with numerous irregular thecal plates, then reduced and approximating to Blastoid regularity. Finally an immediate ancestor of Cysto-Blastoid structure exhibiting an ill-defined separation between calyx and stalk (*cf.* Cystoidea, viii., xviii.), but with fixed pentameral symmetry and composition of the firm cup, as in Blastoids\*, from the Basals upwards (*Stephanocrinus*, ii.). From such an ancestor, after development of arms, the Monocyclica and Dicyclica, distinguished at first only by the exclusion, or inclusion, of Infra-Basals in the cup (*i. e.* the position of the growth-zone), diverged. I pursue further only the Dicyclie series, and neglect the Camerata.

Cambrian.—The primitive Inadunate: 5 simple arms, distinct from the cup; disk firmly plated with 5 Deltoids (Orals), supporting ambulacra above their conjoined edges (*cf.* *Hybocrinus*, xxxvi.). Slightly modified, this type survived among Ordovician Cyathocrinoids (*Porocrinus*, lxxxvi.): Anal plates (X & RA) present in the circle of Radials; Posterior Oral, the only madreporite.

\* The stereotyped monocyclic constitution, sharply separated stalk, and late geological development of Blastoids suggest that this group may be composed, in reality, of *pædogenic* Crinoids, and it would be worth while to extend this hypothesis to some of the Cystids themselves.

Ordovician.—Dendrocrinoid modification. Arms still non-pinnulate, but dichotomously branched; the disk now flexible by interpolation of small plates between Orals and Radials, but Ambulacra remain suprateminal. Anals as before, supporting a great anal turret (xxvi.). Madreporite lost.

Silurian.—Dendrocrinoid arms forked and pinnulate (*Dendrocrinus*, iii.).

Devonian. } Dendrocrinoids lose RA, and then X from cup (*Graphiocrinus* and *Erisocrinus*, c); their arms become biserial;  
Carboniferous. } Infrabasals reduced and covered by stem.

Trias.—From Graphiocrinidae arise Pentacrinidae: cup (patina) shallow, the disk bulging up between the arms; no persistent proximal columnal as yet; stem cirriferous, its ossicles changing from round to pentagonal, with petaloid furrows and radiating ridges; no Anal; arms (again?) uniserial. Various members of the family swim about, and re-anchor themselves by distal cirri of stem. Obscurely leading to Flexibilia Pinnata, but exact links missing (cf. *Bathycrinus*, with bi-fasciate stem-ossicles, like Bourgueticrinidae and Antedonidae, figs. xlix., cxv.).

Jurassic.—The first "Pinnata," with persistent proximal columnal and reduced Basals; stem-ossicles of modified Pentacrinid or Bathycrinid types. *Millericrinus* (no cirri) broke away from bottom of its stalk for swimming, the stem being slowly absorbed (lii.). *Thiolliericrinus*, the first Antedonid, with cirriferous compound Centrodorsal, fairly stout stem, and bifasciate joints of stem-ossicles.

Lias.—*Antedon* and later types break away from top of stalk early in life.

With this sketch of the adult ancestry of *Antedon* before us, let us now see how it is recapitulated in the ontogeny. Certain sequences of form-change take place in the same order. The larva on fixation exhibits successively an armless ("Cystid") stage, and stages with simple arms, forked arms, and pinnulate arms respectively; the Oral plates at first are co-extensive with the disk, as in Blastoids\* and Cyathocrinoids, and then a peripheral growth-zone (perisome) is established between them and the Radials as in Ordovician Dendrocrinoids; an Anal plate appears within the circlet of Radials, rises above it and disappears, as in Carboniferous Dendrocrinoids; the Infra-Basals arise separately and then fuse with one another and the proximal columnal, marking the change from Dendrocrinoidea to Flexibilia Pinnata.

\* Another Blastoid or pre-Crinoid relic appears to be involved in the abortive attempt of the 5 primary tentacles to branch and grow as radial canals in the vestibulate stage, each peristomial tentacle (in spite of its lack of food-grooves and skeleton) representing a Blastoid brachiole. If Blastoid brachioles are homologous with Crinoid pinnules, the view that simple unbranched arms are primitive in Crinoids becomes untenable.

Now note the discrepancies. Except possibly in the anal interradius, there is no trace of præ-Cambrian irregularity in the number and arrangement of the skeletal plates, of the earlier acquisition of radial symmetry by the ambulacra and its later imposition upon the plates of the calyx; no sign of the derivation of the stalk by constriction of a pyriform base; no evidence of the oral plates having originally formed a solid disk, above the sutures of which the ambulacra ran. Except for certain additional dislocations to be referred to in a moment, it is just as in the development of the skeleton of a Vertebrate limb: the number of the skeletal elements is fixed from the beginning (even the pattern of the stem-joints) and ontogeny reveals no signs of their past history—with two exceptions: the migrations of the Anal plate and the composition of the Centro-dorsal. The former is a precious record of the change exhibited by the ancestral Dendrocrinoids, when, as arm-structure changed and flexibility increased, the diminishing anal chimney (fig. iii.) no longer required a buttress in the calyx wall to support it. But its retention in the ontogeny of *Antedon* is no proof of the normality of so precise a record of ancestral change: rather is it the exception which proves the rule of absence of such records. It is comparable with the “useless” notochord of the Vertebrate embryo. It has no part to play in the adult, because, as growth proceeds, the bases of the arms take over the main support of the body; but in the larva the patina is the sole support, and, as an Anal plate (and a Radial as well) was a constant inherited element of the cup through nearly the whole of Palæozoic time, it is scarcely surprising that it should be retained in that part of the life-cycle where it is still conceivably useful. On the other hand, it is squeezed out of the cup as soon as the anal tube, by remaining small, withdraws any demand for its retention, and when the flexible incorporation of the five arm-bases in the cup sets up a counter-demand for strict pentameral symmetry. This demand, so far as the Radial is concerned, has long since been met by the complete elimination of that plate from the ontogeny. “One thing at a time” is nature’s rule. Similarly the ontogenetic history of the Centrodorsal is a physical necessity if one plate is to be made by the amalgamation of a number (*cf.* development of vertebræ, pore-plates of *Echinus*, &c.); and the other recapitulative features of the ontogeny (arm-development &c.) are examples of other necessities of differentiation, since you cannot get 2, except by duplicating 1. Adult recapitulation demands that the arm-branches should extend to the full length of the arms (as in Cyathocrinoids) before they reduce themselves alternately to the dimensions of pinnules. This they do not do. They take the shortest route to their goal, so far as constitution, not ancestry, will allow them.

But these discrepancies with phylogeny are trifles beside the phenomena of development of the Oral and Radial plates. In the whole series of adult ancestors from Cambrian times to the present, not one possessed Oral plates

which rested on the Basals; nor, if we overlook this developmental modification, did one of those ancestors in its adult condition ever possess Orals which were hinged to the Radials on the edge of the cup, capable of opening and shutting over the entire disk like the valves of a trap-door (Bather, fig. xxxiii.; MacBride, 1914, figs. 408-410). Where does the sure, frail "Ariadne-thread" conduct us now? If no fossil evidence were available, anyone who should attempt to reconstruct the ancestral Crinoid on the common embryological assumption that the stalked larva of *Antedon* represented an ancestral adult stage would go inevitably astray, as many have done already in spite of paleontological knowledge\*. For the remarkable thing is that several existing Crinoids possess an arrangement of oral valves in the adult precisely or closely similar to that of the larval *Antedon* (*Holopus*, l.c. xxxiv.; *Hyocrinus*, Sedgwick, 1909, fig. 209; *Thaumatoocrinus*, Carpenter, 1884, pls. iii., vi., lvi.). The relations of the oral plates in *Antedon* to the vestibular roof of the larva, as well as the temporary suppression of Radials, are clearly "conogenetic" features. If a vestibule was a feature in the development of the earliest Crinoids, the oral plates must have been deposited beneath its floor, and not in its roof. Their relation to the roof (which alone enables them to split apart and function as valves) is an embryonic mutation. It is, therefore, scarcely open to doubt that the condition of the oral valves in the adult *Holopus* (and *Hyocrinus*?) is due to the retention of a feature that was purely embryonic, not adult, in origin, and that, in this respect, these interesting Crinoids are as "pædomorphic" as any Perennibranchiate Amphibian.

This brings me to my last point. When the common argument is urged that the stalked larva of *Antedon* "recapitulates" the adult stage of its stalked ancestors, it seems to be forgotten that every type of Pelmatozoan, from præ-Cambrian Cystids to the present time, must also have possessed a tiny fixed stage of simple structure following a free-swimming larval life, and that the main features of the skeleton must have been laid down in that, or a still earlier, stage of its ontogeny. It follows from what has been said that the modern Pentaerinoïd larva of *Antedon* is a modification of the corresponding stage of the ancestral ontogeny, not of the adult stage, and that the adult *Antedon* is not an addition to the ontogeny of any preceding Crinoid, but just a modification of the adult phase of the same ontogeny—partly by loss (e.g. anal turret and plates, Oral plates, stalk, &c.), partly by

\* P. H. Carpenter (1884, p. 145) compared the vestibulate condition of *Antedon* with the Camerate condition of *Haploocrinus* (Bather, xxxv.) and the Platycrinidæ (l.c. xl.). It is a tempting suggestion, especially as the Carboniferous Platycrinidæ possessed bifasciate oval stem-ossicles. But these types are Monocyclic; the relations of the "Orals" are only superficially similar, and it is very doubtful if these plates are other than enlarged "proximal ambulacra" (see Bather, pp. 127-129, and fig. xli.).

elaboration of pre-existing structures (arms, stem-ossicles). Nature does not build up a new type by addition or abstraction of "stages," but of organs, or parts of organs \*. Moreover, when she makes a change, she does not do so by altering these organs, or parts of organs, when fixed or rigid, but when plastic and growing. In particular cases this may be late in life, but it is not usually so, and it is not likely to have been so with respect to the patinal skeleton of the Crinoids under consideration. The Anal plate within the circle of Radials is a feature inherited from earliest Silurian ancestors. It is claimed to "recapitulate" an adult feature of those ancestors. I submit that no Anal or other plate was ever interpolated within the patina except in the formative stage of growth when the Radials themselves were loose and unsutured. The first Anal plate that entered the Radial circle from the disk (if that was its origin) must have done so as the result of an embryonic, not an adult, mutation. Once let the towering anal chimney of an adult Dendrocrinoid (*cf.* Bather's fig. iii.) effect a breach in the wall of the patina, and the whole cup would split asunder. Nature underpins when it is safe to do so. She usually builds the foundation first and the superstructure afterwards.

16. The following summary, omitting illustrative detail, recapitulates in closer logical sequence the chief points of this attempt to re-define the foundations of Morphogenetic Law.

#### RECAPITULATION.

- I. Ontogeny is the sequential expression of zygotic powers of cell-division through simple to complex grades of cell-grouping and differentiation.
- II. Phylogeny is the procession of ontogenies along a given phyletic line of modification. It is expressed in terms of adult structure, but the zygotes of successive ontogenies have also undergone a parallel elaboration of nuclear or cytoplasmic structure, or of both, which determines the sequence of the ontogenetic form-changes.
- III. The phyletic succession of adults is the product of successive ontogenies. Ontogeny does not recapitulate Phylogeny: it creates it.
- IV. An individual confronts the world before his ontogenetic processes are completed, and often at a very early period of his life-cycle. Only those individuals reproduce who have survived the ordeal of larval conditions. Adaptation of the larva accordingly plays a prime part in determining the modification of successive ontogenies.

\* *Cf.* Weismann (1904, ii. p. 174): "... it is impossible to compare a particular stage in the embryogenesis of a species with a particular ancestral form. Only the stages of individual organs can be thus compared and parallelized."



- V. The life-cycle is extended, not by addition of a new adult stage at the end of the old adult stage, but by further differentiation of organs or parts of organs. Old adult characters are eliminated from the ontogeny unless required as temporary bases for the new characters.
- VI. As the individual, through all the form-changes of his life-cycle, is an evolutionary and functional unity, modifications manifested in his larval or adult phases involve co-ordinating changes in the more passive and formative phases (embryonic, post-larval, pupal stages).
- VII. Thus, while a given ontogeny, under normal conditions, tends to repeat the form-sequences of its predecessors, it is liable to changes in every part of the life-cycle—positively, by equipping the larval and adult stages for the changing conditions of their various careers, or with greater efficiency for the same conditions, and negatively, by abbreviating the formative processes to the uttermost.
- VIII. The idea that form-changes in ontogeny were preceded by similar changes in adult ancestry is an illusion, since adult Metazoan ancestors never directly gave rise to their successors, but to gametes; and these, blended with other gametes, were the real heralds of successive ontogenies. Plainly the first Metazoan was not produced by a Metazoan. He was the result of a Protozoan ontogeny, the *tour de force* of a genius among Protozoan zygotes. The first Bird was hatched from a Reptile's egg. We can speak of earlier and later, original and modified, ontogenetic processes; but the possibility of a distinction between ancestral and ontogenetic processes is out of the question. All changes are ontogenetic.
- IX. In the same way the contrast between "palingnetic" (repetitive of adult ancestry) and "cenogenetic" (foreign or non-repetitive) characters, which was originally based by Haeckel on an assumed hereditary difference between adult changes and embryonic adaptations, has lost its significance. Both types of character were of ontogenetic origin, and equally hereditary, but the one set arose earlier in the phyletic history than the other. Morphology will not recover exactitude of outlook until it is entirely freed from the hypnotic influence of Haeckel's terminology. I propose in future to use *palæogenetic* and *neogenetic* when referring to ontogenetic processes, and *palæomorphie* and *neomorphie* when contrasting primitive and modified types of structure.
- X. There is a general correspondence between the successive grades of differentiation in ontogeny and the successive types of organisation which characterise the steps of phyletic progress (Meckel's law). This general correspondence exists because each series—the ontogenetic and the phyletic—was preceded and caused by the same

phylogenetic series of ontogenies. The outcome of each successive ontogeny was an adult representative of one of the successive types of organisation. The last ontogeny of the whole series is the one under consideration. Inevitably there is recapitulation of successive grades of differentiation, but repetition of adult ancestral stages is necessarily and entirely lacking. Ontogeny is not an animated cinema show of ancestral portraits; but zygotes may be likened to conjurers playing the old tricks for the most part, and occasionally opening a surprise packet—nor do they always keep their novelties back until the end of the performance, as *Antedon* and *Holopus* bear witness.

In other articles I propose to deal with the origin and significance of larval forms, and to draw attention to some further examples of the influence of larval characters upon adult organisation, to which I apply the term "Pædomorphosis."

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On the Terrestrial Isopod *Eluma cælatum* (Miers) = *purpurascens*, Budde-Lund. By WALTER E. COLLINGE, D.Sc., F.L.S., Keeper of the Yorkshire Museum, York.

(PLATE 8.)

[Read 15th June, 1922.]

THE genus *Eluma* was described by Budde-Lund \* in 1885 for a species of Terrestrial Isopod which he named *E. purpurascens*. The description of both the genus and species is imperfect, and no figures accompany it.

As a doubtful synonym Budde-Lund gives the *Armadillidium cælatum* of Miers, which was described and figured by Miers in 1877 from specimens obtained at Cayenne, French Guiana, South America †.

A careful comparison of the description and figures, both imperfect, with specimens received from Mr. D. R. Pack-Beresford, from the Hill of Howth, Co. Dublin, Ireland, leaves no doubt, in my mind, as to the identity of Miers's species with these. His specific name *cælatum* therefore has priority, and must replace that of *purpurascens*.

Neither Miers or Budde-Lund gave any figures of the structure, and their references are very brief and in some points scarcely accurate; I am therefore venturing to redescribe and figure the genus and species.

Mr. Pack-Beresford ‡ figures the external appearance of this species, but his illustrations are not correct in all details. Verhoeff § has given two figures of parts of the exoskeleton.

The *Rhacodes inscriptus* of Koch ||, regarded by Dollfus and Budde-Lund as a synonym of *Tylos latreillei*, Aud. & Sav., was thought by Eaton ¶ to be referable to this species.

#### *ELUMA, Budde-Lund.*

Body oblong-ovate, strongly convex, setose, and closely and minutely punctured. Cephalon strongly marginate, with median and lateral lobes; epistome with sloping dorsal portion and keeled. Eyes simple, very small. Antennulæ small, 3-jointed, terminal joint conical. Antennæ somewhat short, flagellum bi-articulate. Pleural plates of mesosomatic segments 2-7 slightly excavate anteriorly, ventral margin indented on segments 2-4, truncate on 6-7. Coxopodite of first segment separated from the pleuron and

\* Crust. Isop. Terr. 1885, p. 48.

† Proc. Zool. Soc. Lond. 1877, p. 665, pl. 67. figs. 3-3 b.

‡ Irish. Nat. 1908, p. 255, pl. 10.

§ Arch. f. Biontologie, 1908, Bd. ii. p. 371.

|| In Rosenhauer's 'Die Thiere Andalusiens,' 1850, p. 422.

¶ Ann. & Mag. Nat. Hist. 1882 (s. 5), vol. x. p. 360.

forming a notch on the posterior margin. Telson triangular, width greater than the length, not extending beyond the uropoda. Uropoda short, extending slightly beyond the telson; basipodite robust, thickened, antero-dorsal surface expanded, articulating ventro-anteriorly; exopodite flattened, expanded, laminate: endopodite styliform, elongated.

This genus is undoubtedly most nearly related to the genus *Armadillidium*, Brandt, as is readily seen in the form of the body generally, in the structure of the cephalon and its appendages, and in the form of the uropoda and telson. It differs, however, from *Armadillidium* in the following characters:—The cephalic lobes are more feebly developed and the epistome is keeled in the middle line, and has a sloping dorsal portion, and auricula-shaped prominences above and lateral to the antennal sockets; the eyes are small and simple; the pleural plate of the first mesomatic segment exhibits a notch on the posterior angle formed by the protrusion of the coxopodite; finally the uropoda extend beyond the telson.

In the sloping dorsal portion of the epistome and in the form of the first mesosomatic segment, there is a resemblance to the condition found in certain South African Cubaridæ.

**ELUMA CÆLATUM (Miers). (Pl. 8. figs. 1–12.)**

*Armadillidium cælatum*, Miers, Proc. Zool. Soc. Lond. 1877, p. 665, pl. 67. figs. 3–3*b*.

*Eluma purpurascens*, Budde-Lund, Prosp. gen. spec. Crust. Isop. Terr. 1879, p. 6; Crust. Isop. Terr. 1885, p. 48.

" " Dollfus, Ann. Soc. Espan. Hist. Nat. 1892, xxi. p. 164; 3 Congrès Inter. Zool., Leyden, 1895, p. 357; Mém. Soc. Zool. France, 1906, ix. p. 528.

" " Norman, Ann. & Mag. Nat. Hist. 1899 (s. 7), iii. p. 69.

" " Verhoeff, Arch. f. Biontologie, 1908, ii. p. 371, t. 31. figs. 68, 69.

" " Pack-Beresford, Irish Nat. 1908, p. 255, pl. 10.

" " Pack-Beresford & Foster, Proc. Roy. Irish Acad. 1911, xxix. (s. B), p. 185, pl. 8. figs. 4*a–b*.

*Eluma cælatum*, Collinge, Check-List Brit. Terr. Isop. 1917, p. 115.

Body oblong-oval, strongly convex, smooth and somewhat shiny, minutely punctured, clothed with short, thick setæ. Cephalon (figs. 1 & 2) strongly marginate anteriorly, median lobe extending beyond the lateral lobes, which are small; epistome with sloping dorsal portion and keeled in the median line, with auricula-shaped prominences above and lateral to the antennal sockets. Eyes simple, very small. Antennulæ (fig. 3) small, 3-jointed, with three or four short setæ on the side of the third joint. Antennæ (fig. 4) somewhat short, 1st joint small, 2–4 almost subequal, 5th elongated; flagellum biarticulate, proximal joint less than half the length of the distal one, with fine terminal style. First maxillæ (fig. 5) with the outer lobe terminating in ten spines, the first three of which are strong and curved, the 4th, 5th, and

6th smaller, the 7th a long fine spine, 8th and 9th very small, 9th and 10th faintly denticulate, setose on the outer border of the lobe; inner lobe prolonged on the outer side terminally, with two short setose spines. Maxillipedes (fig. 6) with comparatively small lobes, outer lobe 3-jointed, 1st joint short, with two large spines, 2nd joint also with two large spines, 3rd joint terminating in a number of spinous processes; inner lobe with a single long pointed spine, and two tooth-like spines towards the inner border. The segments of the mesosome (figs. 7-9) strongly convex, subequal, pleural plate of the 1st segment flanking the cephalon, anteriorly, strongly curved, lateral margin thickened, posterior angle notched. Pleural plates of 2nd to 7th segments excavate anteriorly, ventral margin of 2nd to 4th indented, 6th to 7th truncate. Uropoda (figs. 10 & 11) short, but longer than wide, extending beyond the telson; basipodite robust and thickened, antero-dorsal surface expanded, articulating ventro-anteriorly; exopodite flattened, expanded, and laminate, protruding on the inner side: endopodite styliform, longer than the exopodite, widest just above the middle, with terminal setaceous pad and spinous setæ. Telson (fig. 12) roughly triangular, with rounded apex, width greater than the length, not extending beyond the pleural plates of the last segment of the metasome.

Length 11.5 mm.

Colour (in alcohol) a light coffee-brown.

*Hab.* Hill of Howth, Co. Dublin, Ireland (*H. R. Pack-Beresford*).

In the figure given by Mr. Pack-Beresford (*op. cit.* pl. 10) the distal joint of the flagellum of the antennæ is too short and no style is shown, whilst the pleural plates of the metasome are scarcely long enough; further, the last segment extends more posteriorly than is shown in his figure (*cf.* Pl. 8. fig. 12).

The distribution of this species is as yet only very imperfectly known. It was originally described from Cayenne, French Guiana, South America. Budde-Lund \* says it is "commonest in the Island of Madeira." . . . "I have seen some from Cayenne taken by Don Gelski." . . . "Two specimens taken by Professor Reinhardt in the Island of Nicobar, and determined by † Cl. Krøyer under the name of *Armadillidium purpurascens*, are preserved in the Museum at Copenhagen." ‡.

Dollfus § records it from many localities. He states:—"The genus *Eluma* is entirely Western, and contains only one species, *E. purpurascens*, B.-L., a woodlouse of a purple-red colour, remarkable for its simple eyes. Very abundant in the Atlantic archipelagos, in the Canaries, the Azores, and Madeira; it occurs again at Cintra (Portugal), and in Western Algeria, but

\* Crust. Isop. Terr. 1885, p. 48.

† Mr. Pack-Beresford (*op. cit.* p. 257) translates this described by.

‡ Dr. K. Stephenson has very kindly referred to these specimens and sent me notes thereon.

§ 3 Congrès Intern. Zool., Leyden, 1895, p. 357.

the most curious fact about it is its range northwards to the French Department of Les Charentes, where it is acclimatised from Angoulême to Royan (very common twenty years ago in this locality, it has become much rarer lately), and southwards to Cayenne!" (The Cayenne here quoted would appear to be in France, and must not be confused with Miers's original locality.) The same author records it from Constantina in the Sierra Morena (Spain), and states, with reference to the record for the French Department of Les Charentes \*, "où il a été certainement introduit," but gives no reason for this supposition.

Norman † records it from Madeira, where he found it "up to heights of between 2000 and 3000 feet."

Finally, Mr. Pack-Beresford (*op. cit.*) has recorded it from the Hill of Howth and Portmarnock, Co. Dublin, Ireland.

The allied species *E. helleri*, Verhoeff, is from the Island of Teneriffe.

#### EXPLANATION OF PLATE 8.

Illustrating Dr. Walter E. Collinge's paper "On the Terrestrial Isopod *Eluma cælatum* (Miers)."

*Eluma cælatum* (Miers).

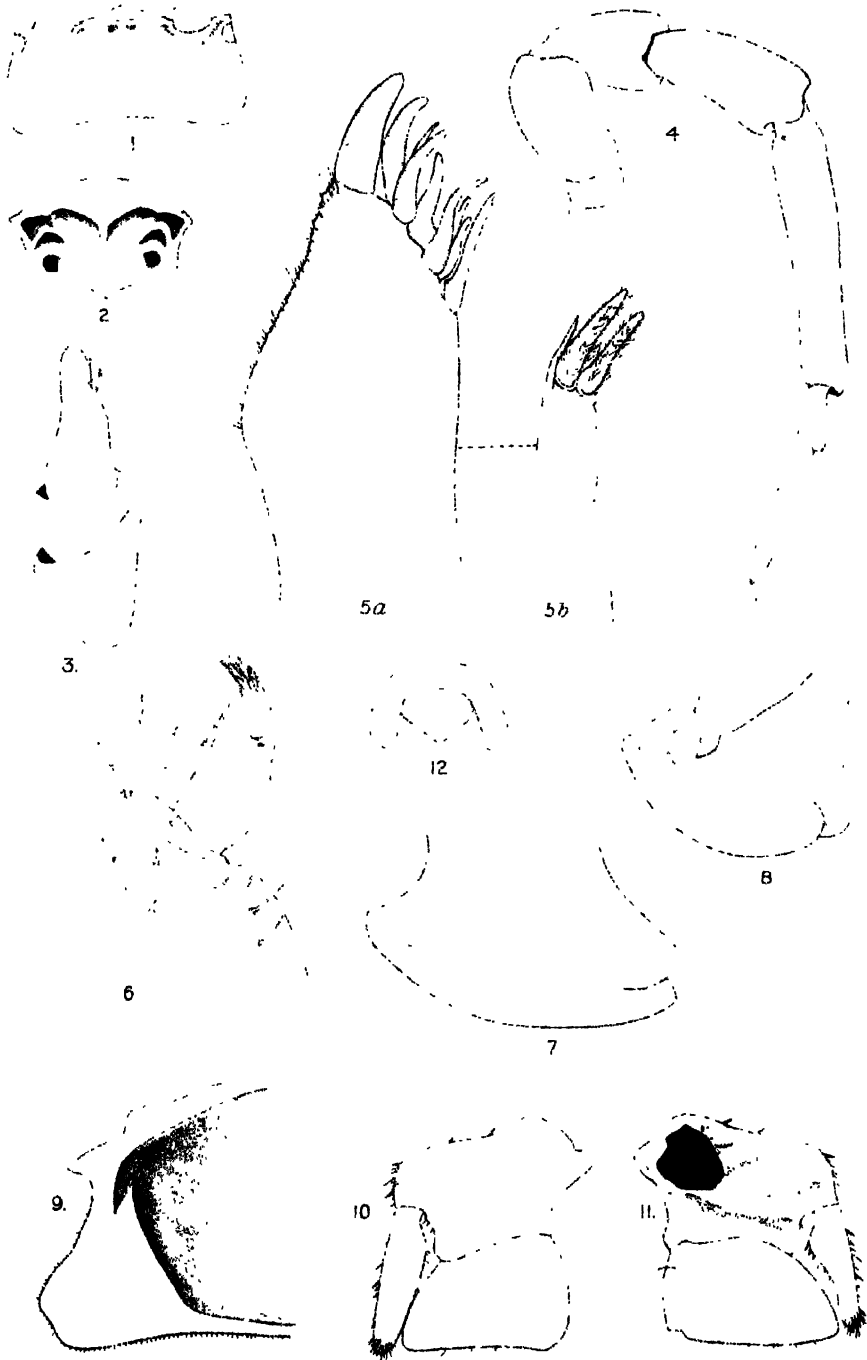
- Fig. 1. Dorsal view of the cephalon.  $\times 10$ .  
 2. Anterior view of the cephalon.  $\times 7.5$ .  
 3. Antennule.  $\times 110$ .  
 4. Right antenna.  
 5. Terminal portions of the inner and outer lobes of the right first maxilla.  $\times 56$ .  
 6. " portion of the left maxillipede.  $\times 56$ .  
 7. External view of the pleural plate of the first mesosomatic segment.  
 8. Internal view of the pleural plate of the first mesosomatic segment.  
 9. " " lateral portion of the second mesosomatic segment.  
 10. Right uropod, dorsal view.  
 11. " " ventral view.  
 12. Last metasomatic segment and telson.  $\times 8$ .

The Author desires to thank the Carnegie Trust for the Universities of Scotland for a grant to defray the artist's charges.

\* Ann. Soc. Espan. Hist. Nat. 1892, xxi. p. 164.

† Ann. & Mag. Nat. Hist. 1899 (s. 7), iii. p. 69.





Æ J.J. Del. ad nat.

JT Reuss Reid Lith. Edin<sup>r</sup>

ELUMA CAELATUM (MIERS)



On two new Terrestrial Isopods from Madagascar. By WALTER E. COLLINGE,  
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(PLATE 9.)

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I. INTRODUCTION.

FOR the privilege of examining the very interesting specimens of Terrestrial Isopods here described, I am indebted to the kindness of my friend Dr. W. T. Calman, of the British Museum (Natural History). The material was collected in Madagascar in 1911 by the Hon. Paul A. Methuen.

There is a single specimen referable to the genus *Alloniscus*, Dana, not hitherto described, remarkable for its great size; and a further very interesting new species, for the reception of which I have constituted a new genus, to which I have given the name of *Calmanesia* in honour of Dr. W. T. Calman.

II. THE ISOPODEAN FAUNA OF MADAGASCAR.

Very little attention has been paid to the Terrestrial Isopods of Madagascar. Buddle-Lund (3) has described certain species in the collection of the Berlin Museum. Dollfus (8) in 1889 described the *Porcellio cristatus*, placed by Buddle-Lund in the genus *Lyprobius* and later in the genus *Nagara*. The same author in 1895 (9) described a further series of species, amongst which

there were four new species of *Alloniscus*; these Budde-Lund placed in a new genus, *Diacara*, for reasons which are not altogether clear; there are certainly slight differences in the form of the uropods, but these are scarcely sufficient to warrant generic distinction. In 1908 (4) Budde-Lund published his memoir on the Isopoda of Madagascar and East Africa, in which he described and partly figured nine further new species, re-describing and partly figuring other known forms. No figures, however, are given of *Periscyphops praeconius* and *Armadillo horridus*. According to this author, there are known from Madagascar thirty-two species referable to twenty genera.

If, as is generally supposed, Madagascar represents a part of a great submerged southern continent, then we should expect to find representatives of South-Eastern and South-Western genera, but whether owing to long isolation these forms have changed or died out, it is remarkable that the bulk of the known forms show affinities rather with Northern forms than with Southern ones, and they further seem to have little relationship with the South African genera. Hitherto no genus has been found peculiar to Madagascar; the new genus *Calmanesia*, here described, is therefore of more than usual interest. Until, however, we know much more of the fauna of this island, it is futile to speculate.

### III. DESCRIPTION OF *ALLONISCUS NACREUS*, sp. nov.

#### *ALLONISCUS*, Dana.

This genus as yet is only imperfectly understood, and the members are subject to a wide range of variation. It occurs in North and South America, India, Siam, the Malay Peninsula, South Africa, Sumatra, Java, and the Maldive, Hawaiian, Nicobar, and Celebes Islands. *Arhina*, Collge. (6) is a closely-allied genus from India.

Of the twenty-one described species of *Alloniscus*, seven are known to occur in Madagascar, viz.: *A. alluaudi*, Dollf., *A. elegans*, Dollf., *A. guttatus*, Dollf., *A. tigris*, Dollf., *A. brevis*, Budde-Lund, *A. pallidulus*, Budde-L., and *A. pigmentatus*, Budde-L.

#### *ALLONISCUS NACREUS*, sp. nov. (Pl. 9. figs. 1-12.)

Body broadly oval, strongly convex, irregularly pitted, finely sculptured on each side of the mesosome. Cephalon (figs. 2 & 3) medium size, convex above, frontal margin distinct, lateral lobes small; epistome slightly depressed, with prominence between the antennæ. Eyes oval, dorso-lateral. Antennulæ (fig. 4) small, curved, and 3-jointed, the terminal joint with a number of bristle-like setæ on the inner side. Antennæ (fig. 5) short, joints gradually enlarging from the 1st to 4th, 5th joint elongated and more

slender; flagellum 3-jointed, with short terminal style. First maxillæ (fig. 6): outer lobe terminating in four stout spines and six smaller ones, with stout setæ on the outer margin of the appendage. Second maxillæ (fig. 7) thin and plate-like, with terminal bifurcation, densely setose. The segments of the mesosome are strongly convex and finely pitted, with lateral sculpturing; pleural plates with terminal margin more or less truncate, posterior margin of the 5th, 6th, and 7th slightly produced backward. Maxillipedes (fig. 8) rather narrow; outer lobe 3-jointed, with two spines on the first joint, two tufts of spines on the second, and a single terminal tuft on the third; the inner lobe is somewhat conical and surmounted with numerous small setæ. Appendages of mesosome (fig. 9) stout and strongly spinous. Metasome comparatively small, segments 3-5 with pleural plates directed backward and inwards. Uropoda (figs. 10 & 11) short, extending beyond the telson, basal plate sparsely covered with setæ; exopodite sickle-shaped; endopodite slender, terminating in three long setæ. Telson (fig. 12) triangular, lateral margins slightly rounded, apex subacute, with slight depression above.

Length 19 mm.

Colour (in alcohol) creamy white.

*Hab.* Tamatave, East coast of Madagascar (*Herschell & Chaurin*).

This fine species is the largest member of the genus yet described. Apart from this feature, it conforms with the essential characters of the genus.

#### IV. DESCRIPTION OF THE GENUS *CALMANESIA*.

*CALMANESIA*, gen. nov.

Body oblong-oval, capable of partly rolling into a ball. Segments of mesosome and metasome with a series of long-jointed spines. Cephalon with lateral and median lobes. Antennulæ very small. Antennæ elongated; flagellum 2-jointed. Pleural plates, excepting those of the first segment, drawn out into a long spinous process. Uropoda small and without endopodites. Telson short and obtuse, not extending beyond the uropoda.

*CALMANESIA METHUENI*, sp. nov. (Pl. 9. figs. 13-25.)

Body oblong-oval, covered with elongated jointed spines. Cephalon (figs. 14 & 15) short, slightly convex dorsally, frontal margin distinct, with lateral and median lobes; seven spines on the dorsal surface: epistome slightly convex. Eyes situated dorso-laterally, facets few and large. Antennulæ (fig. 16) small, 3-jointed, middle joint very small. Antennæ (fig. 17) elongated, 1st joint small, 2nd and 3rd larger, 4th and 5th greatly elongated; flagellum 2-jointed, distal joint rather longer than the proximal one, with terminal bunch of setæ. First maxillæ (fig. 18): outer lobe with six short

spines, of which the outermost is the largest and has a short, stunted tooth-like body at its base; on the inner side is a single needle-like spine; densely setose on the outer margin; inner lobe small, with two elongated setose spines terminally. Second maxillæ thin and plate-like, setose terminally. Segments of the mesosome strongly arched, the 1st with eleven jointed spines and the remainder with seven; pleural plates, excepting those of the 1st segment, produced into long spinous processes. Maxillipedes (fig. 19) somewhat robust; outer lobe 3-jointed, with two straight spines on the 1st joint, four on the 2nd, and one small one on the outer border of the 3rd joint, which latter terminates as a blunt process surmounted by a number of setæ; inner lobe plate-like, with two small tooth-like spines and a single straight spine on the ventral face. Appendages of the mesosome (fig. 20) comparatively short. Segments of the metasome crowded together, 3rd, 4th, and 5th each with two jointed spines in the mid-dorsal line: pleural plates greatly elongated, directed backward and terminating in a finely drawn out spine. Uropoda (fig. 24) extending beyond the telson, basal plate oval-shaped, with a single appendage (exopodite) which terminates in a strong curved spine. Telson (fig. 25) somewhat triangular in shape, terminally obtusely pointed, with two 3-jointed spines and a small median papilla in front of these.

Length 10 mm.

Colour (in alcohol) creamy white with dark chocolate-coloured markings. Younger forms creamy white.

*Hab.* Forest of Fohohy, East Madagascar, 1911 (*Herschell & Chaurin*); Ánalamazotra, Eastern Forest, June 1911. Under rotten logs (*P. A. Methuen*). The specimens from the latter locality are evidently immature.

a. *General Form.*—This is undoubtedly one of the most handsome and peculiar Terrestrial Isopods known, rivalling in both form and colour any species hitherto described. The long-jointed spines covering the mesosome and metasome and the drawn-out spinous pleural plates give the animal the appearance of some Coleopterous larva rather than a Crustacean.

There is, I think, little doubt but that the members of this genus are capable of rolling themselves up into a ball like the Armadillidiidæ. Apart from the fact that one specimen was found (in alcohol) so rolled up, the extreme mobility of the segments support such a view.

The remarkable jointed spines on the body would seem to be a hitherto undescribed character in the Isopoda. I have been unable to find any reference to such in the literature on these Crustaceans. So far as I can make out from the material available, the spines first appear as small excrescences on the surface of the segments (fig. 23, a); these increase in size and later appear as ordinary spinous processes (fig. 23, b); a little later they continue to grow, a distinct joint forming at the base of the first period of growth (fig. 23, c), and this continues until, with the exception of those

on the cephalon and telson, where the spines are 3-jointed, they become 4-jointed, the longest measuring 6.5 mm. (fig. 21). All the spines are covered with minute scales like the rest of the body (fig. 22). There are seven spines on the cephalon, eleven on the first mesosomatic segment, seven on the second to seventh segments, and two on each of the last three metasomatic segments and the telson.

b. *The Cephalon*.—This is extremely narrow from before backwards and slightly convex. Anteriorly there is a well-marked marginal ridge which laterally develops into the two lateral lobes, and in the middle into the median lobe. Posteriorly the margin is deeply excavate, and from the middle line a strong spine arises; lateral to this there are a pair of spines on each side, and a single one on each side, slightly nearer the centre, in front of the former. All of these spines are 3-jointed. The epistome is slightly convex dorsally and distinctly so ventrally, whilst laterally the sockets for the articulation of the antennæ stand out as conspicuous bodies.

1. *The Eyes* are placed dorso-laterally; they are of medium size and with few but large facets.

2. *The Antennular* (fig. 16) are small, and consist of an elongated basal joint, a tiny ring-like middle joint, and a gradually tapering terminal one. At the distal end of the third joint and on the inner side are two blunt papillæ.

3. *The Antennæ* (fig. 17) are greatly elongated. The first joint is small, and the second about two and a half times as long, the third is still longer and narrower, whilst the fourth and fifth are almost coequal and nearly as long as the second and third together. All the segments are covered with minute setæ. The flagellum is 2-jointed, the distal joint being rather longer than the proximal one, and terminates in a bunch of elongate setæ.

4. *Oral Appendages* (figs. 18 & 19).—These afford very little assistance in placing this genus and species. The 2nd maxillæ and the maxillipedes are of the usual type. The 1st maxillæ in the form of the first tooth of the outer lobe differs somewhat from any other genus.

c. *The Mesosome*.—The segments of the mesosome are strongly arched. There are eleven jointed spines on the first segment and seven on the remainder.

1. *The Pleural Plates* of the first segment are broad plate-like bodies with rounded anterior and posterior angles; anteriorly they bound the postero-lateral half of the cephalon. Those of segments 2–4 are somewhat triangular in shape, the apex of the triangle being drawn out in a fine curved spine: the whole of the plate is curved, the free spinous end bending upward. On segments 5–7 the plates terminate more abruptly before the commencement of the spine, and they are rather flatter.

2. *Appendages*.—The walking limbs are comparatively short, and of a less robust type than in most genera of Oniscidæ.

d. *The Metasome*.—The segments of the metasome are crowded together, the 1st and 2nd being scarcely visible in a dorsal view and without pleural plates. Of the remaining three the last is the smallest. The pleural plates are of a similar type to those of the last three metasomatic segments. There are a pair of jointed spines on each of the last three segments.

1. *Uropoda*.—The uropoda extend beyond the telson. The basal plate is somewhat oval in shape and has a fold on its posterior side. Only a single appendage appears to be present, which is slightly longer than the width of the basal plate and terminates in a strong curved spine. I take this appendage to represent the exopodite.

2. *Telson*.—The telson is comparatively small, somewhat triangular in shape, and terminating in an obtuse point. It bears a pair of 3-jointed spines and a median papilla anteriorly and between the bases of the spines.

#### V. AFFINITIES.

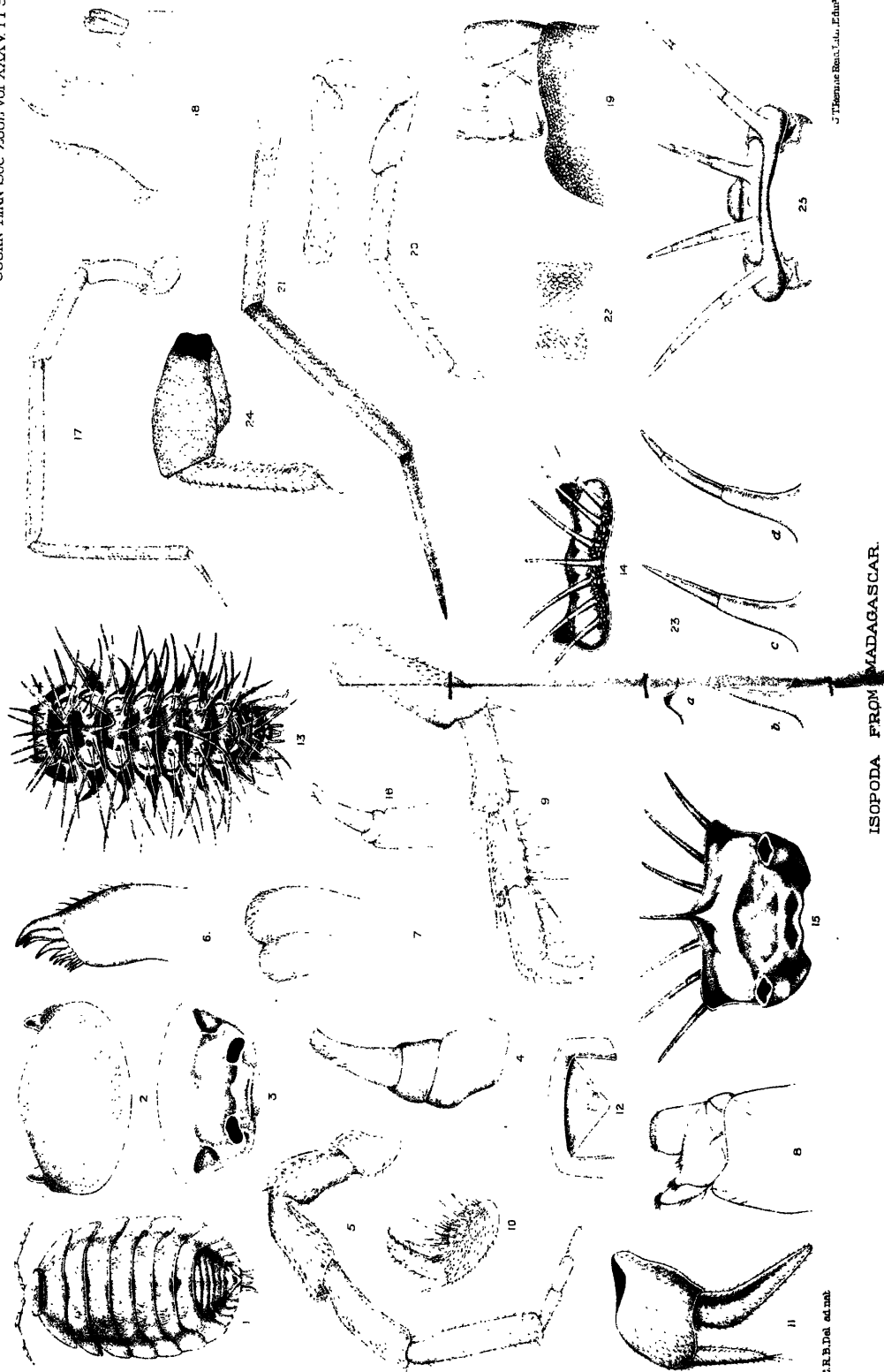
The genus *Calmanesia* appears to be widely separated from any known genus, and at present we must leave it without attempting to relegate it to its proper position in the classification.

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## EXPLANATION OF PLATE 9.

Illustrating Dr. Walter E. Collinge's paper "On Two new Terrestrial Isopods from Madagascar."

- Fig. 1. Dorsal view of *Alloniscus nacreus*, sp. nov.  $\times 3$ .
2. " " the cephalon.  $\times 12$ .
3. Anterior view of the cephalon.  $\times 12$ .
4. Left antennule.  $\times 50$ .
5. Right antenna.  $\times 25$ .
6. Terminal portion of the inner lobe of the left 1st maxilla, ventral view.  $\times 80$ .
7. " " left 2nd maxilla, ventral view.  $\times 80$ .
8. " " right maxilliped, ventral view.  $\times 80$ .
9. Second thoracic appendage, dorsal view.  $\times 25$ .
10. Ventral surface of the terminal portion of the 2nd thoracic appendage, showing spinous area.  $\times 25$ .
11. Dorsal view of the right uropod.  $\times 25$ .
12. " " the telson and last metastomatic segment.  $\times 10$ .
13. Dorsal view of *Calmunesia methueni*, gen. et sp. nov.  $\times 6$ .
14. " " the cephalon.  $\times 20$ .
15. Anterior view of the cephalon.  $\times 20$ .
16. Left antennule.  $\times 80$ .
17. Right antenna.  $\times 20$ .
18. Terminal portion of the inner and outer lobes of the right 1st maxilla, ventral view.  $\times 80$ .
19. Terminal portion of the right maxilliped, ventral view.  $\times 75$ .
20. Second thoracic appendage, dorsal view.  $\times 20$ .
21. Jointed spine from off the mesosome.  $\times 20$ .
22. Portion of same, showing the scales.  $\times 80$ .
23. a–d. Stages in the development of one of the jointed spines.
24. Dorsal view of the right uropod.  $\times 50$ .
25. Terminal segment of the metasome and telson, seen from the anterior.  $\times 20$ .

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On the Mouth-parts of the Shore Crab. By I. A. BORRADAILE, Sc.D.  
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Zoology in the University. (Communicated by Professor E. S.  
GOODRICH, M.A., F.R.S.)

(PLATES 10, 11.)

[Read 6th April, 1922.]

## I.

THE organs which stand about the mouth of a Decapod Crustacean make up a complex as intricate as any that is to be found in the Animal kingdom. They are also extremely important to their possessor, for without them the animal can neither feed nor breathe, and to one of them falls, at least in many cases, the duty of keeping clean the indispensable organs of special sense. Yet they are at present but little understood.

In a study upon the Common Prawn, published in 1917 (5), I endeavoured to solve the problem which the morphology of these organs presents, and made a beginning with the investigation of their working. This paper contains an account of some observations upon *Carcinus maenas*, a species at the other end of the decapod series.

The term "mouth-parts" denotes, in the Crab, a number of organs which stand upon the under side of the body, in the region which is bounded behind by the anterior edge of the mass of fused postoral sterna, at the sides by the edge of the inturned carapace where this encloses the exhalant passage of the gill-chamber, and in front by the fused antennal and mandibular sterna (epistome). The sterna of the maxillary to second maxillipedal segments inclusive are more intimately united with one another than those of the legs; and they form a mass, roughly triangular with the apex forwards, that stands out steeply from an area, in front of and beside it, which is covered by a thin cuticle supported upon the pieces of the endophragmal skeleton. It is upon this area that the mouth-parts are inserted. They are: the six pairs of limbs from the mandibles to the third maxillipeds inclusive, the upper lip or labrum, the lower lip or metastoma, and the fleshy opening of the mouth itself. I propose to describe in succession each of these parts and its movements, and then to discuss the functions of the complex as a whole.

## II.

1. *The Third Maxilliped* is built upon the plan of the legs. This statement, by a phenomenon often seen in serially homologous structures, is true even of features—such as the fusion of the basis and ischium and the nature of the articulation of the joints—which cannot be supposed to have existed in the schizopod ancestor whose thoracic limbs were not differentiated from one

another. The limb is a broad structure, flattened in that direction which is morphologically antero-posterior, and widened from side to side. In what may be called the *normal position* it is turned forwards till its wide plane passes the horizontal and slopes a little upward in front. In this position it meets its fellow on the middle line, and the two form an operculum which almost wholly encloses the mouth-field, abutting behind on the sterna, at the sides upon the edge of the carapace, and in front upon the epistome save in the middle, where a gap is left through which the gill-stream can flow even when the operculum is most tightly closed. Each third maxilliped *articulates* ventrally with the hinder angle of its sternum, and dorsally (anteriorly) with the epimerite of its segment.

The *coxa* is of oval transverse section. Its proximal rim bears on the under side the knob which makes articulation with the sternum, where it is received by a saddle-shaped hollow between two processes. Adjoining this is a facet on the median surface of the joint, which works against the external (antero-lateral) face of the sternum. On the dorsal side the rim bears a socket which articulates with a correspondingly shaped process of the epimerite. On the outer side the coxa has a backward-curving flange, to which, by a flexible suture, is hinged the *epipodite*. This organ has a stout base, which bears on the dorsal side the small podobranch, and a long, blade-like process which, diving under the edge of the branchiostegite, enters the gill-chamber and passes between the posterior arthrobranch of its own limb and the anterior arthrobranch of the cheliped, to lie between the gills and the side of the body. The whole organ, and the flange upon which it is borne, is spirally twisted, so that, starting in the horizontal plane in which the main part of the limb lies below the mouth, it ends in a vertical plane against the flank. The flange and the base of the epipodite stand in that gap, between the anterior face of the coxa of the cheliped and the branchiostegite, which is the anterior inhalent opening of the gill-chamber; and their twisted shape bears such a relation to the opening that when the maxillipeds are in the normal position they lie across it and almost but not quite close it, but when the maxillipeds are divaricated, the epipodites lie in the midst of the opening, with their flat sides parallel to the stream, to which they offer little opposition. The part of the opening which is covered when the maxillipeds are approximated is the anterior. The extent to which the hinder part remains open varies with the position of the cheliped.

The *basis* and *ischium* are fused, though traces of their junction usually remain in the form of a groove. By this it is shown that the basis is a small region which in width makes the transition from the stout coxa to the flat ischium, and in position fills a triangular gap between them, due to the fact that the ischium is displaced to the median side of the coxa. The free (median) edge of the basis abuts upon the edge of the sternum, and continues the contact made by the facet upon the coxa. On the outer side the basis bears

the *exopodite*. The stem of this is a long, narrow, flattened structure, directed forwards between the endopodite and the branchiostegite, and bearing at its end a flagellum which is directed inwards above the merus towards the middle line. The flagellum consists of a basal joint, and a many-jointed lash, curved with the concave side forwards. The exopodite stands at the junction of basi-ischium and coxa, and besides being articulated to the former is attached by membrane to the latter.

The ischium is an oblong, roughly rectangular, and very flat joint, which makes nearly half the total surface of the limb. It is succeeded by the *merus*, a flat, subquadrate structure, stouter than the ischium and tilted a little outwards upon the latter. Owing to its stouter form it has a median face in place of an edge, and upon this face, which is hollowed, is set the carpus. That joint, with the two which succeed it, forms a subcylindrical, tapering *palp*, which can be stretched out so as to be roughly in line with the axis of the basi-ischium and merus, but in the normal position is folded back against the hollow face of the merus. In this position the palps fill the gap which would otherwise be formed by the outward tilting of the merus, and thus complete the operculum.

As has been mentioned, the *mode of articulation of the joints* is that which is found in the legs. At the proximal end of each, the rim of the hard cuticle is raised, at two points on opposite sides, into articular processes which, bridging over the arthrodial membrane, play against corresponding surfaces on the distal rim of the preceding joint; and these articular surfaces are so shaped as to limit the movement of the distal of the two joints to a particular direction. Since, however, this plane is a different one in each joint, the limb as a whole has a good deal of mobility, though owing to its shape and position the third maxilliped is less freely movable than the legs. I have not thought it necessary to give details of the articulations of the several joints, but particulars of the movements they permit will be found below. They are modifications of those of the segments of the legs.

A remarkable feature of the third maxilliped is the way in which it is completely outlined with *hairs*, set along the edges of its flat surfaces. Most of these hairs are feathered in one way or another. They are short where the edge is, in the normal position, apposed to some other structure, but long on that part of the anterior (morphologically external) edge of the merus and carpus over which the gill-stream flows. Along the median edge of the ischium there run on the lower (ventrally-facing) side two narrow parallel bands of hairs with a naked, convex strip between them. These hairs are stout, with a close, stiff feathering on all sides. The actual edge is finely but bluntly toothed. On the inner or dorsal (morphologically anterior) side of this joint there is a row of hair-tufts near the median edge, and a rather sparse band of hairs near the outer edge. The dorsal side of each of the last three joints is covered with long, and stiff, serrated bristles. The epipodite



is fringed on both edges with long hairs, and the ventral (hinder) surface of the flange of the coxa upon which it stands is very hairy. The flagellum of the exopodite bears a fringe of long, feathered hairs, many of them jointed. A more detailed description of the hair-system of this and other limbs of the Shore Crab is given by McIntosh (11). With its functions I will deal later.

The *cuticle* of the third maxilliped, except the flagellum and the blade of the epipodite, is hard and pigmented, like that of the rest of the exposed surfaces of the body. In this respect it contrasts strongly with that of the other mouth-parts.

The *muscular system* of the third maxilliped closely resembles that described by Pearson (13) for the same limb of the Edible Crab, and I have not examined it further than was necessary to assure me of this fact. Each of the joints of the limb has a flexor and an extensor muscle, those of the coxa and basi-ischium arising from the endophragmal skeleton and being inserted by conspicuous tendons, those of the remaining joints arising each from the joint preceding that upon which it is inserted. The exopodite has flexor and extensor muscles for the stem, which they enter from the coxa; but the flagellum has an extensor only, and must be brought back into the flexed position by its elasticity. The epipodite possesses muscles, but its most important movements are probably those which it carries out passively, under the action of the powerful muscles of the coxa.

The *action of the flexors and extensors* of the coxa is to draw the whole limb to and from the normal position, in which its median edge meets that of its fellow on the middle line. In moving outward it passes a little ventrally, so that it clears the sub-branchial region of the carapace. This movement at the same time uncovers both the mouth-field and the inhalent opening of the gill-chamber, and sweeps the epipodite under the gills, as I will explain later. The movements of the basi-ischium are more complex. They may be analysed into: (a) a movement to and from the middle line independently of the movement of the coxa, (b) a dorso-ventral rotation, like the letting down of a flap, (c) a rotation about a longitudinal axis on the outer side of the limb, like the opening of a door, (d) a divarication of endopodite from exopodite. This latter movement must be due to a contraction of the extensor muscle of the exopodite simultaneously with that of the flexors of the basi-ischium, for this bears the exopodite and tends to carry it in its own direction. The other movements of this joint are more difficult to understand, since they seem to take place with a good deal of independence, and the muscular apparatus does not appear to be adequate for this. Actually, they are performed together, combined into a single sweeping movement whose direction is decided by the form of the articulation between basi-ischium and coxa, but a compensating movement of the coxæ can keep the edges of the two limbs together, so that they are let down as a flap without at the same time necessarily opening as a pair of doors, though

their planes are now directed obliquely and meet ventrally at an angle. The articulation is, moreover, not absolutely rigid, and the movements may therefore perhaps be modified by the small additional flexor muscle described by Pearson. The merus, of course, shares the movements with the basi-ischium, but it is capable of a moderate amount of rotation upon its articulation with the latter. The rotation is oblique, from within outwards and at the same time dorso-ventrally. It is not conspicuous in the living crab, but it is used sometimes to lower only the distal half of the operculum, and sometimes to give free play to the movements of the palp. The joints of that organ can move upon one another, but it is generally flexed or extended rather stiffly as a whole. It is so articulated that in extension it moves upwards as well as forwards. The flagellum of the exopodite is flicked outwards and inwards with very great rapidity, so that at times it cannot be followed by the eye. I have already alluded to the movements of the epipodite.

2. *The Second Maxilliped* resembles the third in general plan, but differs from it greatly in appearance on account of the following features:—It is smaller, and its cuticle is thinner. In the *endopodite*, the basi-ischiopodite is short and its components are easily recognizable, the merus is very long, and both, though flat, like the rest of the limb, are narrow. Actually they are narrower than the last three joints, which are more flattened than those of the third maxilliped. The *exopodite* is as large as that of the third maxilliped, and much longer than its own endopodite. It is grooved to fit against the edge of the branchiostegite. The *epipodite* is not hinged to the coxa, and a supporting rod of chitin runs from that joint along its anterior edge. It bears a long podobranch, and its distal part enters the gill-chamber, passes between its own arthrobranch and the anterior arthrobranch of the third maxilliped, and lies, like the epipodite of that limb, within the gills. The second maxilliped has the same *relations to the sternum and epimeral region* as the third, but is not connected with them by articulations like those of the latter limb.

The second maxilliped is not outlined with *hairs* like the third, but a good deal of long hair is developed upon it, especially on the hinder face of the basal joints, on the epipodite, along the outer and towards the end of the inner edge of the merus, at the end of each of the last three joints, and on the outer edge of the exopodite. The end of the last joint bears about eight very strong spines. The inner edge of the merus is not toothed. On the basal joints, and on the exopodite, the hairs are scathered.

The *musculature* of the second maxilliped resembles that of the third, but the limb is more mobile.

3. *The First Maxilliped* is a thin, flat limb, covered for the most part with delicate cuticle, from which the majority of the articulations have disappeared. The *coxa* is a short, broad region, whose entity is established by

the presence, on the anterior side, of a rod-like sclerite, which runs across it and at its median end expands into the stout cuticle of a large, subpyramidal endite. The apex of this endite is directed dorsally, towards the mouth, and that side of it which is opposed to the sternum forms a facet, above the membranous attachment of the limb. At its outer end, the transverse sclerite articulates with the stout cuticle at the base of the epipodite, and that in turn makes articulation by means of a hard process with the epimerite. I have not been able to find a true articulation on the inner side of the limb. The epipodite, which lies *outside* the gills, is much expanded at its proximal end, especially in a triangular forward lobe. A strong tendon runs along it. The *basipodite* is represented by a soft region distal to the coxa. It bears on the median side a large, flat, forwardly projecting endite or *lacinia*, which has a curved outer and a straight median edge, and is a little concave dorsally (anteriorly), so as to fit over the surface of the mandible. Distally the basis bears the *exopodite*, which resembles that of the second maxilliped, and the *endopodite*, which consists of an unjointed shaft, flattened in a plane which faces obliquely outward and inward, with a triangular distal expansion, flattened in an almost horizontal plane and separated from the shaft by a not very flexible suture. This expansion completes in front the exhalent channel of the gill-chamber. Its median edge is turned ventrally and lies against the anterior side of the mandible.

The limb is outlined with stout *cuticle*, which also passes along the sutures between the protopodite and the exopodite, endopodite, and endites. Its relation to the sternal and epimeral regions resembles that of the second maxilliped, but at the base of the epipodite there lies, as has been mentioned, a rather ill-developed articulation, which is not present in the limb behind it.

A row of long, flexible *hairs* follows the outer edge of the exopodite, the distal and inner edges of the endopodite, and the outer edge of the large endite. On the inner edge of this endite the hairs are more numerous, shorter, and rather stouter. The proximal endite is covered with long hairs, all directed towards the mouth. On the exopodite, the inner edge of the endopodite, and the outer edge of the large endite the hairs are feathered.

Flexor and extensor *muscles* of the coxa move the limb as a whole. The exopodite has a musculature like that of the third maxilliped, and the endites have muscles of their own. The epipodite has a system of three powerful muscles.

The limb can be *moved* to and from the middle line of the body, doubtless by means of the muscles of the coxa. In moving outwards it also travels a little backwards. The large endite makes independent movements, rotating forward-outwards and inward-backwards and thus with its edge describing an ellipse. Usually it moves inward-backwards towards the mouth when the rest of the limb is rotating outward-backwards, and thus the smaller

endite, which projects towards the mouth, is being drawn away from the latter. When the smaller endite comes forward into the mouth the larger endite moves away from it.

4. *The Maxilla (Second Maxilla)* is a very broad limb, flattened in its distal parts, but with a swollen nucleus representing the main part of the *protopodite*. This region bears on the outer side the large, quadrant-shaped, slanting exopodite or scaphognathite, distally the roughly-ogival, peaked endopodite, and internally the two cleft lobes, representing four endites, which characterise the maxilla of the Decapoda. I have already (5) suggested that the first of these endites belongs to a precoxal segment of the limb, the second to the coxa, and the third and fourth to the basis. The first cleft lobe is in *Carcinus* reduced to a pair of narrow ribbons. The limb is covered with a delicate cuticle, thickened in places to form certain *sclerites*. Across the protopodite there runs on the ventral (morphologically posterior) face, from the junction between the cleft lobes to the base of the limb at its outer side, a raised ridge, strengthened by a sclerite which probably represents the coxa. At its outer end this abuts upon a longitudinal piece which caps the side of the swollen nucleus of the limb, and which is sutured to, but not definitely articulated with, the epimerite. More distally, the protopodite is crossed by an irregular M-shaped, transverse ridge, strengthened by two sclerites, each of the form of an inverted V, which are hinged to one another where they meet at the apex of the M. This appears to represent the distal limit of the basis. On the dorsal (anterior) face of the limb a longitudinal ridge, strengthened by a sclerite which roughly corresponds in position to the outer member of the M on the opposite face of the appendage, partly separates exopodite from protopodite. On the anterior face of the *scaphognathite* are two sheets of stout cuticle, with thickened edges, which support it and provide for the insertion of the accessory muscles. The maxilla is seated upon the membranous body-wall, in front of the sternum, upon which it does not abut. It is attached by membrane only, except at its outer end, where, as mentioned above, one of its sclerites is joined by a flexible suture to the epimeral region.

The hairs which in a prawn fringe the whole edge of the scaphognathite are here found at its anterior and posterior returning edges only. As in the prawn, they are feathered. The endopodite is fringed with long, silky hairs, but these are feathered only at the base of the outer edge. The ends of the cleft lobes bear relatively short, and, for the most part, simple hairs.

The swollen base of the maxilla harbours a complicated and relatively powerful *musculature*. According to Pearson (13), whose account is, I think, applicable to *Carcinus*, there are in *Cancer* two extensors and two flexors of the coxa, and four "extensors" and four "flexors" of the scaphognathite. It would perhaps be preferable to call these muscles abductors and adductors respectively, since they draw the limb downwards from the side of

the body and upwards towards it. They arise from the endophragmal skeleton, and are inserted on the base of the scaphognathite. In its anterior part, the scaphognathite is crossed, at right angles to its long axis, by half-a-dozen bands of muscle, which, pulling downwards, curve its surface. These are the "accessory muscles." They arise from the sclerites of the basal portion of the limb, and are inserted on the anterior of those which support the scaphognathite. A feeble strand of muscle runs across the base of the endopodite to the second cleft lobe, but independent movements of these structures, if they take place at all, are insignificant.

The *movement* of the maxilla consists in a flapping of the scaphognathite to and from the roof of the exhalent passage of the gill-chamber. It is carried out in two ways, according as the current is being directed backward or forward. To drive the water forward, the posterior and outer end of the scaphognathite is smartly applied (presumably by the "outer flexors") to the roof. Then the accessory muscles, which have been keeping the organ curved, allow the flexors to bring the remainder of it into the same position, with the undulating movement described by Garstang (8). Finally, it is drawn downwards by the extensors, being at the same time curved by the accessory muscles, so that it becomes concave towards the roof. To drive the water backward this procedure is reversed. The bending of the scaphognathite which it involves is facilitated by the fact that the two supporting sclerites of that organ are united by a flexible region. It seems possible that the function of the muscles of the coxa is to hold firm the protopodite when the accessory muscles contract. The lobes of the median edge of the limb may be seen to be drawn passively to and fro with each stroke of the scaphognathite.

5. *The Maxillule (First Maxilla)* is a small limb, flattened and curved to fit against the surface of the mandible, and composed of three inwardly-directed lobes—the inner and outer laciniae and the endopodite—and an external basal portion which unites them. It is usual to regard the laciniae as representing the coxa and basis, but, as I have elsewhere argued (5), the *proximal lacinia* is probably the gnathopase, or endite of the true first segment of the Crustacean limb, "the 'precoxa' or 'pleuropodite,' which may or may not have originally existed as a free joint in every biramous limb, but has now nearly always disappeared, either by fusion with the trunk or with the second joint (coxa or coxopodite), or perhaps sometimes by exclamation." In the maxilla it is represented by one of the components of the first cleft lobe. This lacinia is narrow and strong, and curves backward and dorsally to enter the mouth, at the hinder end of the mandible. Its base is widened and is continued across the face of the limb as a ridge, covered partly with thin cuticle but supported by a sclerite, and projecting anteriorly. Towards its outer end this ridge turns backwards (posteriorly), with a suture in the sclerite which supports it, and dies away upon the stout articular sclerite,

with which its sclerite makes a narrow articulation. The second segment of the limb, the true coxa, is represented by the region which connects the two laciniae. For the most part it is covered with soft cuticle, but its outer side is strengthened by a stout bar, the *articular sclerite* just alluded to. This runs along the outer side of the basal portion of the limb. Proximally it articulates with a hard piece upon the epimeral region; near this it is joined by the sclerite of the precoxal ridge; distally it has a swelling with which the sclerite of the basipoditic (outer lacinial) ridge articulates. On this swelling stands a tuft of very long setae, which may be called the "coxopoditic setae." The *outer lacinia* is much larger than the inner, and its end is expanded and has roughly the same shape as the large distal endite of the first maxilliped. Like the inner lacinia it is prolonged as a ridge across the face of the limb, but the ridge has no projection of its anterior edge and its sclerite makes a better articulation with the articular sclerite. It represents the basipodite. The *endopodite* has a wide base and a narrow, strap-like, blunt-ended continuation, separated by a suture. When the limb is *in situ*, this strap passes in a remarkable way over the shoulder of the mandible, lying in a notch, much as the endopodite of the maxillule of the Prawn is carried in a notch on the edge of the metastoma.

The maxillule is *attached* in a little depression of the body-wall immediately behind the mandible. Like the maxilla it does not abut upon the sternum. It has an external but not a median articulation.

Besides the coxopoditic setae, which are very long, strong, and thread-like, the limb bears on the outside of the endopodite a small patch of feathered *hairs*, at the end of the endopodite another such patch, and on the inner edge of the endopodite a fringe of long silky hairs. The laciniae bear on their free ends a mass of very strong spines, which on the tip of the inner lacinia are curved in the same direction as the lacinia itself. The *cuticle* of the endopodite and basal region is thin, but on the laciniae and their ridges and the articular sclerite it is of considerable strength.

Pearson (13) describes in the maxillule of *Cancer* four muscles—two outer and two inner, a "flexor" and an "extensor" in each pair, the flexors arising from the protogastric region of the carapace and the extensors from the endopleurites of the endophragmal skeleton. In *Carcinus* six strands of muscle enter the maxillule. Of these, two are inserted on the articular sclerite, one at each end of the sclerite of the outer lacinia, and two on the sclerite of the inner lacinia, at the base and near the middle. This set of muscles appears to be adapted to move the whole appendage inward and outward, and to rock each lacinia to and fro in an antero-posterior direction. There is also a band of muscle running from the sclerite of the outer lacinia to the middle of the broad part of the endopodite. I believe that this when it contracts pulls the lacinia forwards towards the endopodite, which is firmly strapped to the mandible by its narrow end.

The laciniae are capable of independent *movement*. The outer moves to and from the middle line and also forwards and backwards in the body, and it combines these movements in varying degrees. The inner moves in and out of the mouth.

6. The *Mandible* is a short limb, whose proximal region or *body* is widened athwart the body of the crab and very strongly calcified. This region, which may represent either the coxa or precoxa, but is more probably both combined, is divided into two portions which it is convenient to know as the "head" and the "apophysis." The junction between these is marked by deep notches on the anterior and hinder sides and by an oblique, inflexible suture which joins them. The *apophysis* appears to run deep into the body, but it is in reality not internal like the pieces of the endophragmal skeleton but an external structure, the true base of the limb, which pushes in the membranous body-wall till it comes to lie in a deep, close-fitting pocket. It presents to this pocket a convex anterior face and to the interior of the body a deeply concave posterior face. Upon its edges are inserted the muscles which move the limb. The *head* is much deeper from before backwards than the apophysis, and convex ventrally. It expands towards the middle line, where it presents to its fellow a sharp cutting or "incisor" edge, in the middle of which is an obsolescent tooth. Dorsal to the cutting-edge, in its concavity, is a low mound, the "molar process." External to this, also on the dorsal side, is a process with an outwardly facing concavity which articulates with a knob on the epistome. External to the articular process, and still on the dorsal face of the limb, is inserted the *palp*, an inwardly-curved structure, which should be composed of three joints but actually has only two, because the first and second have fused. In the normal position it is folded back above the limb and almost hidden. The joints of the palp are flattened, the second more than the first. The limb articulates in front with the epistome, and behind is flexibly sutured to the sclerite which supports the metastoma.

External to the base of the palp is a group of feathered *hairs*. The palp itself is bordered with rather long hairs, which are feathered at its base but stout and simple at its apex. There is also a patch of sparse hairs on the ventral face of the apophysis.

The *musculature* of the mandible resembles that described for *Cancer* by Pearson. There are four muscles. A large outer adductor, inserted by a broad tendon upon the outer angle of the apophysis, arises from the subhepatic region of the carapace, and by its contraction must pull the end of the apophysis downwards and so bring its cutting-edge upwards and inwards against that of the other mandible. An inner adductor arising from the dorsal carapace is inserted by a very long tendon near the inner end of the mandible, which it must pull directly upwards. Two abductors, inserted respectively near the outer angle and on the posterior border of the

apophysis, will pull that part of the limb upwards and so rotate the cutting-edge downwards and outwards.

The sole movement of the head of the mandible is a rotation upon its articulation which alternately parts the incisor edges, opening them like a pair of doors, and brings them together. The palp is extended and flexed, digging its apex into the space between the incisor edge and the flank of the labrum.

7. *The Metastoma* is a fleshy structure which lies behind the mouth, between the mandibles and the maxillules. It has two forwardly-directed lobes, the *paragnatha*, which stand wide apart against the mandibles, covering the notches on the hinder side of the latter between the head and the apophysis. The paragnatha are joined by a low transverse cushion, a little raised in the middle, on the border of the mouth. The whole is supported on each side by a sclerite which follows its base and at the end is sutured to the mandibles. The paragnatha contain some glandular tissue, but are not muscular and appear to be moved only passively.

8. *The Labrum* is a large, fleshy lobe which forms the anterior border of the mouth. Its base is rounded and swollen in front but narrows behind, where it projects into the mouth. Distally it is produced behind into a nose-like process which overhangs the mouth. Its exposed (ventral) wall is strengthened by a triangular sclerite. Its sides are moulded to fit closely against the dorsal faces of the mandibles when the palps are flexed against them. It contains, besides a good deal of glandular tissue, much muscle, notably in two longitudinal bands. Its movements are hard to observe, since it has not so sharp an outline as the limbs and is only exposed when the mandibles part, but they appear to consist chiefly in a tucking of the nose into the mouth and its withdrawal.

9. *The Mouth* lies above the hinder end of the mandibles. It is a longitudinal slit, which forks in front owing to the projection into it of the base of the labrum, and behind owing to the low median prominence of the metastoma. To it converge all the surrounding structures—the nose of the labrum, the mandibular palps, the inflected hinder angle of the incisor edge of the mandible, the inner lacinia of the maxillule, and the pyramidal endite of the first maxilliped. All these are so formed as to make entry to the mouth easy but egress from it very difficult.

### III.

1. *The functions of the mouth-parts* are threefold. They subserve respiration by keeping a stream of water flowing through the gill-chamber and hindering particles from lodging upon the gills; they subserve alimentation by tearing up the food and thrusting it into the mouth; and one of them, the third maxillipeds, cleans the eyes, antennules, and antennæ.

2. *The branchial chamber* of the crab is no less complex and specialized



than the rest of the organisation of that animal. In its widest sense, the term may be applied to the whole of the very large space that lies between the flank of the body and the over-arching fold of the carapace known as the branchiostegite, which encloses the chamber above, and without, and partly below. The flank itself constitutes the inner wall of the chamber. Of the two layers which compose the branchiostegal fold, the outer is hard and calcified, that which is towards the chamber is membranous. In their hinder region the two layers are not widely separated, and there are between them only blood-vessels and connective tissue; but anteriorly certain viscera intrude into the upper part of the fold. The hard layer of the branchiostegite lies at first almost horizontal, so as to form a roof above the chamber and the intruding viscera. It is then turned downwards at an angle, which in the hinder region is obtuse but becomes more and more acute as it is followed forwards, to form a wall which curves inwards till it reaches the flank of the body above the bases of the limbs. As the angle at which this wall joins the roof becomes more acute, the wall faces more downwards, till in the fore part of the body a portion of it becomes horizontal; there it forms a floor to the chamber. The shape of the chamber is of course determined not by the contour of the outer layer of the branchiostegite, but by that of the inner. This layer makes in the hinder part of the thorax a continuous curve from above downwards, constituting an arched inner roof to the chamber, which has here no floor properly so called. In front, however, where the outer wall becomes horizontal, the inner wall turns inward at an angle to line the floor of the chamber. In the thoracic part of the latter, the floor underlies the overhanging part of certain gills which project considerably above the bases of the limbs. In the head, it closes from below the exhalent chamber shortly to be described. A number of "dorso-ventral muscles" enable the membranous roof to be raised or lowered.

The chamber is sharply divided into two parts—a true "gill-chamber" in the thoracic region, and an "exhalent passage" or "prebranchial chamber" in the cephalic region. Of these divisions the *gill-chamber* is much the larger in every dimension. Its inner wall is battered back so as to face upwards as well as outwards, and is brittle, though thin, and composed of broad ribs—the so-called "epimera"—one to each limb from the last leg to the second maxilliped inclusive. That which lies above the cheliped is larger than the rest and prominent. Those behind it face a little backwards and those in front face forwards, so that the whole wall is convex outwards, forming a low, roughly half-conical mound. In front, the chamber narrows rapidly, its membranous roof at the same time falling steeply to the hinder opening of the *exhalent passage*, where the roof is upheld, and the opening maintained, by an arching, calcified sclerite. Here the roof turns forward as that of the exhalent passage. This is a shallow chamber which diminishes in width as the carapace narrows forwards. Its inner wall has become merged in the

roof, so that it has only roof and floor. Shallow though this channel is, the effective depth of its entrance is lessened by a double barrier. One component of this is the epipodite of the first maxilliped, which, sweeping round on its spiral course, roughly parallel with the epipodite of the third maxilliped but starting in front of the gills and lying upon their outer surface, crosses the portal of the exhalent passage in such a way as to bar it from behind and from outside and leave access to it only from above and from within. Since the wide base of the epipodite does not merely touch the floor with its edge but lies flat against it, the movements by which the tail is caused to travel over the gills probably never separate the base from the wall of the passage. The other component of the barrier is the "branchial ridge" of Pearson, a fold of the membranous layer of the floor, parallel with the anterior side of the principal inhalent opening but at a short distance from it, which fits between the podobranch of the second maxilliped and the epipodite of the first and helps to enable the latter to make effective contact with the floor. On the inner side of the exhalent passage, the edge of the branchiostegite does not meet the body closely at the bases of the limbs, but leaves there a long, narrow gap. This is normally filled by the endopodite and exopodite of the first maxilliped and the exopodite of the second, which are moulded longitudinally to fit together and against the mandible and to receive the branchiostegite. Further forward, in front of the mandible, the body-wall, which is here the hinder part (endostome) of the epistome, is concave, and so falls away dorsalwards from the branchiostegite and widens the gap. Thus is formed the *exhalent opening*. It is bordered behind, and contracted, by the expanded end of the endopodite of the first maxilliped, and discharges forwards and towards the middle line, so as to direct the current of its side to the antenna and eye of the opposite side.

The *gills* of *Carcinus* are nine on each side. The second maxilliped has a podobranch and an arthrobranch, the third a podobranch and two arthrobranches, the cheliped two arthrobranches, and the first and second walking-legs each a pleurobranch. Each gill is a tapering structure. Except the podobranch of the second maxilliped, which lies horizontally and is directed backwards at the bases of the maxillipeds in front of the principal inhalent opening, the gills are turned upwards and inwards, and lie against the inner walls of the chamber, converging to its highest point, just before the roof falls in front. They are closely applied to one another and separate a shallow "hypobranchial space" against the inner wall from an "epibranchial space" under the branchiostegites. The gills are phyllobranchs. Each of them, save the arthrobranch of the second maxilliped, is heart-shaped in transverse section, owing to the fact that the leaflets project as lobes above the axis but die into it below. Thus it comes about that where two gills lie side by side there is between them on the under side a "hypobranchial channel," and above each of them is an "epibranchial channel"

along the axis, between the leaflets. The arthrobranch of the second maxilliped has leaflets on the posterior side only, the anterior side, which is applied to the wall of the chamber, being flat; but along its edge an epibranchial channel runs as a gutter. The hypobranchial channels are part of the hypobranchial space and are in communication with one another under the gills, especially at the bases of the latter, which are there a little arched, leaving a longitudinal corridor in which lies normally the epipodite of the third maxilliped. The epibranchial channels are part of the epibranchial space, and will communicate over the gills unless the roof be lowered on to the latter. At the hinder end of the chamber there is a space which contains no gills. This space is very shallow and in it lies the enigmatical fold of the body-wall known as the "pericardial lobe." It is shielded from the current entering over the last leg by a ridge which, as I shall presently show, directs the water forwards and downwards, and it probably plays no important part in the circulation of the water about the gills. The branchiostegite fits closely against the bases of the gills, which are flattened back to receive it. Above most of the rest of the surface of the gills the epibranchial space is probably as a rule deep enough to allow the epipodite of the first maxilliped to play freely, but by the action of the dorso-ventral muscles varies in depth from time to time owing to circumstances of which nothing is known, and which may be related to other functions than respiration. At the anterior end of the chamber, where the arthrobranches of the third maxilliped and cheliped face partly forwards towards the roof as it falls to the opening of the exhalent channel, there is a deeper part of the cavity. Since its roof is flexible like that of the rest of the epibranchial space, it is possible that this does not always exist, but I have always found it, and I believe that it is kept in being, in its lower part at least, by the attachment of the roof to the arched sclerite that I have mentioned. It slants downwards, forwards, and outwards to the opening of the exhalent channel. From it water must be drawn by the action of the scaphognathite into the exhalent channel, which, as I have shown, cannot receive water from the region directly behind itself. Thus the water from all parts of the chamber must pass through this space, and, though it is not sharply defined from the rest of the epibranchial space, it may be distinguished as the "collecting space."

*The gill stream* \*. The water which bathes the gills normally makes *entry* under the edge of the branchiostegite in the thoracic region and leaves in the same way in the preoral region. According to the classical account of this process, given by Milne-Edwards (12), the entry of the water takes place only by an opening which lies in front of the coxa of the cheliped and

\* It was not till I had written the paragraphs on this subject that I saw the paper of Mr. R. K. S. Lim, published in 1918 (10). As my work extends as well as confirms that of Mr. Lim, I have left unaltered what I had written.

external to that of the third maxilliped. Other authors (Bell (1), Giard (7), Bohn (2, 4)) have stated that the water enters above the legs along the whole length of the carapace behind the third maxilliped. Pearson, however (13), finds that in *Cancer* entry is made principally by an anterior opening, which is that of Milne-Edwards, and secondarily by a posterior opening above the last leg, but not between these apertures. An examination of the structures which adjoin the edge of the carapace in *Carcinus* shows (1) a relatively large opening in the position indicated by Milne-Edwards, (2) a smaller opening above each leg, the cheliped included. The openings above the first three walking-legs are separated from one another by meetings between the prominences upon the flank with which the legs articulate and corresponding prominences of the branchiostegal edge. They are longitudinal, and slit-like but well formed. That above the last leg is very narrow, and imperfectly separated from the one in front of it \*, and that above the cheliped is separated from the opening of Milne-Edwards only by a close fitting of the branchiostegite to the coxopodite when the limb is turned forwards. Access to each of the openings above the legs is obtained principally between its coxopodite and that behind it, and by moving the leg backward and upward the crab can almost close it, though at the same time the approach to the orifice above the leg next in front is more widely opened. A large hairy tract on the under face of the branchiostegite has no doubt the function of filtering the water which is drawn through it towards the inhalent openings, and especially that of Milne-Edwards. It rises into a long fringe around a bare patch where the cheliped lies against the branchiostegite, and is there met by fringes on the borders of the cheliped so as to form what is probably a very efficient guard for Milne-Edwards's opening. Along the edge of the branchiostegite another long fringe forms a similar protection for the openings above the legs. By placing with a pipette against each opening a little carmine suspended in sea-water, it may be seen that water enters at all of them, even when the third maxillipeds are opposed so as partly to close with their epipodites Milne-Edwards's opening, and that the water from any opening takes a little longer to reach the exhalent orifice than that from the openings in front of it. When the third maxilliped is divaricated from its fellow, so as to open widely the aperture of Milne-Edwards, water enters there more freely, passing forwards as well as backwards, since the anterior side of the opening is now uncovered, and bathing very copiously the podobranch of the third maxilliped, which has been drawn backward into the full stream. That

\* The crevice above the last leg is continuous with that between the hinder edge of the carapace and the first abdominal segment. Narrow though this opening is, the state of the hairs which line it shows that a little water enters it. No doubt this water flows both ways towards the two gill-chambers. The occasional presence of a little mud in the middle chamber which is connected with the hinder crevice of the carapace proves that water must enter it also, though probably it does not there perform any important function.

podobranch may thus have a greater physiological importance than its size would suggest, though it seems doubtful whether in its more isolated position the water would be drawn between its leaflets. The divarication of the third maxilliped also exposes an opening between it and the limb in front of it which helps to admit water to the fore part of the chamber.

*The course of the water within the gill-chamber* is more difficult to follow, but there can be no doubt that on entering, it passes *under* the gills, that is into the hypobranchial space, then comes outwards between the gill leaflets into the epibranchial space, and finally flows by way of the collecting-space into the exhalent passage. That practically all the water which enters the gill-chamber takes this course, and does not pass directly from the exterior to the epibranchial space, I am convinced by the following considerations :— (1) It is exceedingly unlikely that the blood in the leaflets of the gills is exposed to the stream of water only on their edges, and that their flat surfaces are dependent on eddies or diffusion for the renewal of the water in contact with them. (2) When carmine is caused to enter through any of the openings it is found principally, and the large particles are always found, underneath the gills. (3) The disposition of the parts is such as to suggest that the current flows in the direction that I have described. From each of the openings behind that of Milne-Edwards the shortest route to the exhalent passage leads under and through the gills. If there were a wide space between the gills and the border of the branchiostegite, the resistance due to friction with the leaflets might cause the water to pass over the gills, but actually the branchiostegite fits, as has been said, close against the gill-bases. In front of the cheliped the relations of the parts are different. Here, when the third maxilliped is in its normal position, its coxa and epipodite bar the passage of the water forwards and direct it inwards under the gills; but when the maxilliped is divaricated, the shortest route to the inhalent channel would be, were it not for the barrier formed by the epipodite of the first maxilliped, directly forward. It would then pass partly through the podobranch of the second maxilliped, but in great part between that structure and the floor of the chamber or the bases of the other gills, and would not be distributed to the latter organs, which lie above the direct course. Actually, however, the existence of the barrier mentioned must prevent the water from being chiefly drawn in this direction and cause it to circulate through the upper gills. That the water does actually take the route through the gills can easily be seen by cutting a window in the floor of the exhalent passage and placing carmine in Milne-Edwards's opening. The carmine will be found always to pass under the gills and to reappear above the scaphognathite, not to take the direct route.

The water which enters above the first and second walking-legs flows forwards and inwards along a shallow gutter hollowed on the epimerite *till it reaches the entry of a hypobranchial channel* between the pleurobranch of its

leg and the gill which adjoins it in front ; and through this it passes into the hypobranchial space. The water which enters the opening behind the cheliped flows similarly forward over the arthrobranchial membrane, which is shaped to provide a kind of duct for it, to the entry of the hypobranchial channel between the anterior arthrobranch of the cheliped and the posterior arthrobranch of the third maxilliped\*. At this very large portal of the hypobranchial space it meets the water from Milne-Edwards's opening. From that aperture the current passes, when the third maxillipeds are opposed, obliquely backwards through the portal just mentioned, though a little may stray forwards to pass between the arthrobranches of the third maxilliped. When, however, the maxilliped is divaricated and the opening thus fully uncovered, water passes also to the channels between the arthrobranches of the third and second maxillipeds, and to the podobranchs of those limbs. The water which enters the opening behind the last leg is prevented from flowing directly forwards by a ridge on the epimeral region, passes over the articulation of the last leg, which is not prominent like the others, joins the stream which enters between the last two legs, and reaches the hypobranchial space by passing forwards through a definite entrance formed by the shaping of the hinder leaflets of the last gill at a spot near its base and at the end of the longitudinal corridor mentioned above. The arrangements may be summed up by the statement that the water which enters over each limb passes into the hypobranchial space by an opening between its gill and the gill of the limb in front of it, except that most of the water entering above the third maxilliped passes behind its gills.

*In each hypobranchial channel*, the water flows, I believe, upwards, mingling to some extent under the gills with that in the adjacent channels, and diminishing as it goes by loss between the leaflets of the gills to the epibranchial space. Since this loss is hindered by friction against the leaflets, the water does not all escape till the top of the gills is reached, and is thus distributed over as wide a gill-surface as possible.

The course of the water *over the outer surface of the gills* presents a very difficult problem. The shape of the chamber gives no convincing indication of the direction in which the stream gets through it, and its size, as a whole and in each part, depends upon the changing form of its roof. I can only offer some suggestions on this subject.

Normally, the water will pass direct from the point at which it issues from between the leaflets of the gills to the collecting-space. If, however, the roof be lowered on to the surface of any part of the gills, the water which is passing through them is probably got away by the epibranchial channels. The appearance of these structures strongly suggests that a current flows

\* The entry to the hypobranchial channel between the arthrobranches of the cheliped is very small, and that channel probably receives its water from the longitudinal corridor.

along them. They widen from above downward, and it would at first seem as if the current must flow in that direction. But (1) as each channel widens it grows shallower, so that its capacity is no greater, but rather less; (2) its lower end is probably closed by the edge of the branchiostegite, and in any case leads to a part of the chamber that does not directly communicate with the exhalent passage; and (3) the direction of the leaflets is such as at the lower end to cast the water into the channel in an upward direction. It is therefore probable that the current flows upwards. On the other hand, near the upper end the channel narrows so much that its capacity is greatly diminished, and here the water must be overflowing from it into the space over the gills, which is near the top of the collecting-space. The grooves between the convex surfaces of adjoining gills, which may be known as "interbranchial channels," form a similar system.

All the water enters the exhalent passage from above and within—that is, from the collecting-space. This is due partly to the fact that, as has already been shown, access to the passage from behind is barred, and partly to the fact that the stroke of the scaphognathite is made from below upwards, against the roof; and, as has also been shown, it has the important effect of causing the water to flow through instead of over the gills.

The working of the scaphognathite has already been described. The effective stroke is the upward one, but the downstroke must act upon the water which has entered the lower part of the passage during the upstroke. Probably the bulk of this is driven into the collecting-space and a small portion sent forward to the exhalent orifice.

The stream that issues from each branchial chamber is directed, as has been said, obliquely across the epistome to the opposite side of the front, and often it does in fact take that course. But normally it meets in the middle line the current of the other chamber, and the two deflect one another so that they flow forwards under the antennules. A further modification of the direction of the current is brought about by the activity of the flagella of the maxillipeds. Flicking to and fro extremely rapidly, these exert their force more on the outward stroke when they are drawn by their extensors in the direction of their concavity as a cilium moves than when they are returning by their own elasticity in the direction of their convex sides. They not only reinforce the current very notably, but also turn it outward, and in particular, I think, by means of the hairs with which they are fringed they draw away particles which might otherwise lodge upon the organs of special sense.

The regulation of the gill-stream is brought about in two ways—by alterations in the size of the openings, and by changes in the beat of the scaphognathite and the exopodites of the maxillipeds. I have already shown how the flow through the anterior inhalent opening is regulated by the third maxilliped, and how the legs can close the openings which lie behind them. The size and form of the exhalent opening must also have an important

influence on the current. The aperture is smallest when the third maxillipeds are closely opposed. At such times a steady stream issues from the opening which they leave in the middle of the epistome and flows forwards under the antennules. When a wider opening is necessary, either to provide for a greater flow or to allow the current to be directed to the sides of the body, the operculum may be opened in varying degrees by lowering either the meri only or also the basi-ischia. At such times the form of the exhalent opening proper may be modified by alterations in the position of the expanded end of the endopodite of the first maxilliped.

*The function of the epipodites*\* is the cleaning of the gills. Moving to and fro over the gill-surface they brush it, drag over it their long, flexible, barbed hairs, and thus prevent particles that are brought in by the gill-stream from settling there and closing the minute passages between the leaflets. The importance of this function is shown by an observation of Pearson, who found that in a crab in which the epipodite of one of the first maxillipeds had been destroyed, the outer surface of the gills of its side was covered with a layer of fine mud. In one of my crabs there was a similar deposit of fine sandy particles. In this case the epipodite was intact, but I have no doubt that it was in some way paralyzed †.

By an admirable mechanism the three epipodites, between them, reach almost every part of the gills. The epipodite of the first maxilliped lies *above* the gills and sweeps their outer surface. It is probably moved more by the action of its own powerful muscles than by the excursions of the maxilliped as a whole, which are not extensive, and if they were so would interfere with the other functions of the limb. This epipodite is very flexible, and, doubtless by the action of its muscles, it is kept closely applied to the rounded surface of the gill-mound while it swings upwards and downwards over the gills, describing an arc with its tip. In an almost vertical position it stands against the forward face of the mound. The epipodites of the second and third maxillipeds lie below the gills and sweep the inner surface of the latter. Both are stiffer than that of the first maxilliped. The principal movements of each are probably those which it undergoes passively with the coxa of its limb. These movements can easily be imitated upon a dead specimen, and they must occur with each of the excursions which the limbs are constantly making in life. The epipodite of the second maxilliped lies on the anterior, forwardly-facing region of the inner wall of the gill-chamber. When the maxilliped swings outwards, pivoting on its attachment, the epipodite makes a corresponding inward movement over the face of the thoracic wall, sweeping the inner surfaces of the gills that stand there, with

\* The epipodites of the first and third maxillipeds have also the passive function of directing with their bases the course of the currents in the way that I have already described.

† Since the foreign matter was *above* the gills, it had presumably been brought in during reversals of the current.



which it is almost or quite in contact. As the maxilliped returns, the epipodite is drawn back to its former position. The epipodite of the third maxilliped reaches over the epimeron of the cheliped to lie against the posterior region of the inner wall. When the maxilliped is in the normal position the epipodite lies in the longitudinal corridor at the base of the gills. If the movement of the limb were simply outward, and if the epipodite were not hinged to it, the effect of its divarication from its fellow would be merely to press the epipodite more firmly inward against the wall above the bases of the gills, with which it would therefore tend not to be in close contact. Actually, however, the maxilliped, as I have stated above, rotates downwards as well as outwards, and thus moves its epipodite upwards over the flank of the body, while the movement presently brings the stout base of the epipodite against the articulation of the cheliped, and this opposition flexes it at its hinge and directs it outward as well as upward. Thus when the maxilliped is divaricated, the blade of its epipodite moves upwards and presses outwards against the under surface of the gills, which it sweeps and lifts a little from the thoracic wall, thereby flushing these parts with water. As the maxilliped returns to the normal position, the base of the epipodite is pressed against the arthrobranchs of the cheliped, and thus bent back into the longitudinal direction. The position of the epipodite of the second maxilliped upon the forwardly-facing epimera makes unnecessary any such special mechanism to bring it against the inner surface of the gills.

No doubt the movements of the epipodites have the effect of mingling and distributing the water in the gill-chamber while they clean the gills, but it is not clear that this has any such physiological importance as has been attributed to it.

*The variations of the gill-stream* are a very striking feature of the physiology of the crab. They may be studied either by the carmine method or by watching the movements of the flagella of the exopodites of the maxillipeds, and, after making a window in the branchiostegite, those of the scaphognathite. Since the latter method studies directly the working of the principal agent, it is the most instructive, though it is open to the obvious objection that the action of the scaphognathite is affected by the operation. But when the shock of the latter has passed off, its effects are less serious than might be expected. The most remarkable feature of the action of the scaphognathite is its extreme sensitiveness. Any rough or sudden handling of the crab is liable to cause it to stop—in the face of danger the creature holds its breath. Yet this does not always happen when it is expected. Other variations are brought about by less obvious causes. The scaphognathites work independently, and either of them may cease working while the other continues. Their beating changes its rate and force from time to time in the same individual, and differs in different individuals in the same vessel at the same time. Clearly the causes are sometimes internal: probably

they are often external. From some observations of Bohn (4) on the reversal of the stroke it would appear that the crab is sensitive to changes both in the oxygen-content and in the carbon-dioxide-content of the water. Whether these circumstances act by altering the composition of the blood, or through the sense-organs, or in both ways is not clear. I would hazard a surmise that the third of these alternatives is correct, and from some casual observations I suspect that the antennules are sensitive to oxygen. Changes in the activities of the scaphognathite are accompanied, and its working facilitated, by actions of the subsidiary parts of the apparatus. Probably in the normal, quiet breathing of a resting crab, when the water is clear and perfectly oxygenated, the third maxillipeds are opposed and the flagella of the exopodites at rest. Most commonly, however, at least in experimental conditions, the crab sits with its maxillipeds lowered to some extent. This must have the advantage of lessening the work of the scaphognathite, when a considerable volume of water is being dealt with, by allowing it to get away with less friction; and it also enables the flagella to be brought into play, both to help the scaphognathite, and to drive the current and its contained particles outward, away from the sense-organs. Like the scaphognathite, the flagella may work on one side only or on both at once. One, two, or three of them may work at the same time on each side, and they may give a single stroke or work continuously for long periods. The flagella of one side are complementary to the scaphognathite of the other, driving the current in the same direction, and I have not seen the flagella and scaphognathite of one side both at work while on the other side both are at rest. Further, the maxillipeds may be divaricated. This admits more water to the gill-chamber, admits it where it has a relatively short distance to travel and hence causes relatively little increase in work, and also supplies a set of gills which are out of the main stream when the maxillipeds are apposed. Changes in the posture of the crab have also, as Bohn has pointed out, an effect upon the work of the scaphognathite. When the water is clean and well oxygenated, a horizontal position is possible, though there is always some upcast, at least when the maxillipeds are opposed. But when the water is muddy or foul, the vertical position is necessary to enable reversal of the current to obtain more oxygen, as will presently be shown. The exhalent opening is then often above the surface, and work is heavier while the flow is forward. From time to time the third and second maxillipeds make violent excursions outwards. This happens more frequently when the water is not clear, and it has the effect of sweeping the gills with the epipodites.

From time to time also, the scaphognathite reverses its action, and for a shorter or longer period draws water in at the exhalent opening and drives it backward through the gills and out at the inhalent opening. This is done when foreign particles or distasteful substances are being drawn in, and it is noticeable in carmine experiments when the particles are too coarse. Its

function in this case is obvious. But it also happens at intervals when the water is quite clear and pure. It probably then drives out particles which have gradually accumulated under the gills while the current was flowing in the forward direction and which would in course of time prove harmful. The reversal of the current, which was first studied by Garstang (8, 9) in *Corystes* and other genera, has been examined in *Carcinus* by Bohn (2, 4), who has shown that it always takes place, but varies in frequency and duration with the foulness of and amount of matter in suspension in the water, and that when the water is chemically foul the crab will raise the normally exhalant opening to the surface so that it draws in either the better oxygenated water of the surface or air, which passes out in bubbles at the opening of Milne-Edwards after oxygenating the water in the chamber. These results I can confirm from my own observation. The crabs will live in exceedingly foul water if they be permitted to raise the front of the body out of it, but may be asphyxiated by preventing this. Bohn (4) thinks that the reversal of the scaphognathite has an advantage in resting its muscles. I am not clear that it is necessary to suppose that it has any other function than that of cleaning the chamber and enabling the animal to obtain a better supply of oxygen.

3. In *feeding*, the crab severs the food into morsels which it swallows without finely dividing them. It always seizes the food with the chelæ. The third maxillipeds then part, and the food is placed by the chelæ between the mandibles. If the mass of it be very bulky, one or more of the legs may be brought into action to assist in lifting it and thrusting it towards the mouth. The mandibles part to receive the food, and then close upon it. They do not cut it by a slicing action or chew it, but unless it be soft enough for them at once to sever a morsel of it by pressure, they hold it firm while it is being divided by the action of other organs. If the food be very soft, they may even sometimes be seen to be held wide apart while it is thrust into the mouth by the action of their palps and of the nose of the labrum. Usually, however, the food (I have fed my crabs upon various parts of the body of fishes and upon meat) requires the assistance of other organs for its severance. In this case it is torn by being pulled outwards from the mandibles, much as a crust may be torn by being held with the teeth while the hand wrenches a part of it away. The outward pull is sometimes given by the chelæ, especially if the mass of food be tough, and they often keep a hold upon it when they do not appear actually to be pulling; but most often the work is done by the third maxillipeds, which grasp the food by pressing upon it with the toothed inner edges of their ischiopods and at the same time press downwards upon it with their palps, somewhat as the digit of a sub-chela is closed. These limbs do not cut or chew the food, and rarely pass it towards the mouth, but by pulling it outwards tear from it the portion which is held by the mandibles. The second maxillipeds work in various ways, and their action, like that of the organs in front of them, is often hard

to follow because they are hidden by the third maxillipeds. After the removal of the latter, movements of the inner jaws may be observed, but I have not been able to induce crabs which have been so operated upon to feed\*, and in any case their feeding would not be normal. The second maxillipeds apply to the food their last joints, armed with the strong spines which have been mentioned. With these they sometimes thrust outwards, aiding the third maxillipeds or, if the morsel be small, even taking their place. At other times they appear to be thrusting the food inwards, towards the gape of the mandibles, at others to work up and down upon it, strained as it is between the third maxillipeds and the mandibles, so as to cut through it. It is difficult to discover what is the work of the first maxilliped. The action of the great laciniae would suggest that they are cutting the strand of food, but their armature of bristles is so much feebler than the arrangement of spines upon the dactylopodites of the second maxillipeds and on the laciniae of the maxillule as to throw doubt upon the correctness of this impression. In view of the alternation of their action with that of the pyramidal endites, it seems possible that they are really brushing the frayed portions and fragments of the food backwards towards the opening of the mouth, into which the pyramidal endites help to thrust it. The shape of these endites and of the hairs upon them are such as to make it easy for the food to pass between them into the mouth, but difficult for it to emerge. The maxillae are, I think, quite useless as jaws. Their distal lobes, at least, are feeble, inefficient structures, drawn passively to and fro with the strokes of the scaphognathite. I am less certain about the proximal lobes, but if these have a function I am unable to suggest what it may be. The maxillules are important and relatively powerful structures. I have described the movements of their laciniae. The outer of these cuts at the food with its powerful bristles and the inner, I think, thrusts it into the mouth. Probably in doing so it is cutting or tearing it from the main mass. The paragnatha appear to have the function of closing the notches on the hinder edge of the mandibles, through which the food might work outwards, and of pouring upon it the secretions of their glands, whatever be the functions of these. I have already described the working of the mandibles. I am unable to see that their "molar" faces have any grinding action, but they appear to help to wall in the food which is being thrust into the mouth by the palps, and especially by the action and powerful nose of the labrum. I have been a little surprised, in feeding to the crabs portions of fish and meat containing bone which I should have expected them to be able to crush, to observe that they were rejected, sometimes after being stripped of the softer tissues. It is quite possible, however, that in other circumstances these would have been devoured. After the meal a flurry of the mouth-parts is usually to be seen.

\* Possibly reflexes from these limbs are needed to co-ordinate the movements of the other mouth-parts. A prawn will as readily take food from a pair of forceps as from its own chela. A crab will not.

By brushing their various hairy surfaces against one another they detach the small particles of food that are clinging to them, and these are swept away by strong currents set up by the activity of the exopodites of the maxillipeds.

The *opercular function of the third maxillipeds* deserves mention here. The operculum is not of importance to the crab on account of any part that it plays in feeding. It is freely open during that process, and is not closed again till the mouth-parts have cleaned themselves. It undoubtedly protects the more delicate organs within it, as may be seen by the way in which it is closed when they are approached by any implement. But the closeness of its fitting, and its fringe of hairs, indicate that it is also a part of the respiratory apparatus. The current set up by the scaphognathite is a wonderfully strong one, partly because it is working in a closed system of passages, and there are several places in the neighbourhood of the inner mouth-parts where leakage is probably liable to take place, and throw unnecessary work upon the scaphognathite in keeping up a current of the swiftness which is needed. The closing of the operculum prevents this.

4. *The hairs* which are arranged in so definite a manner upon the limbs play no insignificant part in the events which have just been described. They are of an immense variety. A few particulars about them have been given above, in the course of the descriptions of the limbs, but it is quite impossible to do justice to this subject without devoting to it a special investigation. McIntosh (11) has examined their structure in detail, but their functions still remain to be elucidated. The great majority of the hairs are in some way feathered or toothed, and the lateral members which they then bear may be of every relative dimension and shape, from the finest filaments to the coarsest serration, may vary in different parts of the same hair, be directed at any angle to the axes, or recurved, as on some of the hairs of the epipodites, and be set on one side of it, on two, or on all sides. Most of the hairs are placed on edges or surfaces where they meet the water, either actively in the movement of the limb or passively by the flow of the gill-stream. From their form and position it is clear that they must serve more uses than one, though whether any of them have a double function is less obvious. Some of them undoubtedly serve to *filter* the water entering various orifices. This is clear from the particles with which they may often be seen to be laden. It is notably the function of those which outline the parts of the operculum formed by the third maxilliped, and on its coxa help to guard the opening of Milne-Edwards, as all the openings of the gill-chamber are guarded by hairs on the carapace and on the coxæ of the legs.

Others are *sensory*. Most if not all of these are probably *tactile*, that is give information as to the pressure which is exerted against them, but their sensibility is used in various ways. It is clear from its behaviour that the crab is able to detect the presence of particles in any part of its gill-stream

and accordingly to stop, reverse, or alter its direction. This can only be due to tactile organs at various points in the system. Another use of the tactile sense is involved in the appreciation of the strength of the current, which the animal must possess. Conceivably this might be due to a muscular sense of the power used in producing the current, but, as Dofflein (6) has shown, it is very probable that in Crustacea the muscular sense is supplemented, if not largely replaced, by the information given by tactile hairs brought against the water by the movement of the limbs. In any case, it is likely that this information is possessed by the crab and guides it in the use of its limbs. Probably the more delicately feathered hairs are those which are exposed to and detect finer changes in the pressure of the water. From these there is a gradation to the coarser ones which are used in filtering. Whether any or all of the latter are sensitive does not appear.

Whether, again, any of the pairs sub-serve a chemical sense is doubtful. Certainly the behaviour of the crab shows that it possesses such a sense, and by it is informed of the quality of the water and of the nature of the food. But it is quite possible that this is due to the antennules. Over these the water passes on leaving the gill-chamber, and the juices and debris of the food are rejected towards them, and probably to some extent reach them in spite of or by permission of the exopodites of the maxillipeds. The crab appears, though less clearly than a prawn, to taste as well as to smell its food, but this may be due to the sensibility of the antennule; much as in *Mau*, the aromas of food are appreciated by the olfactory epithelium.

Others of the hairs have a *cleaning* function. This is exercised in very different ways by the long threads on the epipodites of the maxillipeds (and possibly by the coxopoditic setae of the maxillule, for which I can suggest no other function), and by the serrated bristles of the palps of the third maxillipeds. Those organs are continually busy cleaning the various structures in front of them. They brush the antennules, sometimes acting singly, sometimes combing an antennule between them. Each of them brushes the eye and antenna of its side, and reaches across to clean the mouth-parts of the opposite side, attending, for instance, to the delicate and probably sensory hairs of the expanded end of the endopodite of the first maxilliped. In these activities, different parts of the palp are brought each against a different organ, and very possibly the difference in the serration of the bristles in various parts is in correspondence with the structures to be cleaned in the organs to which they are applied.

The function of *current-making* must perhaps be attributed to the hairs on the flagella of the exopodites.

Lastly, the bristles which are used in *manipulating the food* are special members of the series of hairs.

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## EXPLANATION OF THE PLATES.

## PLATE 10.

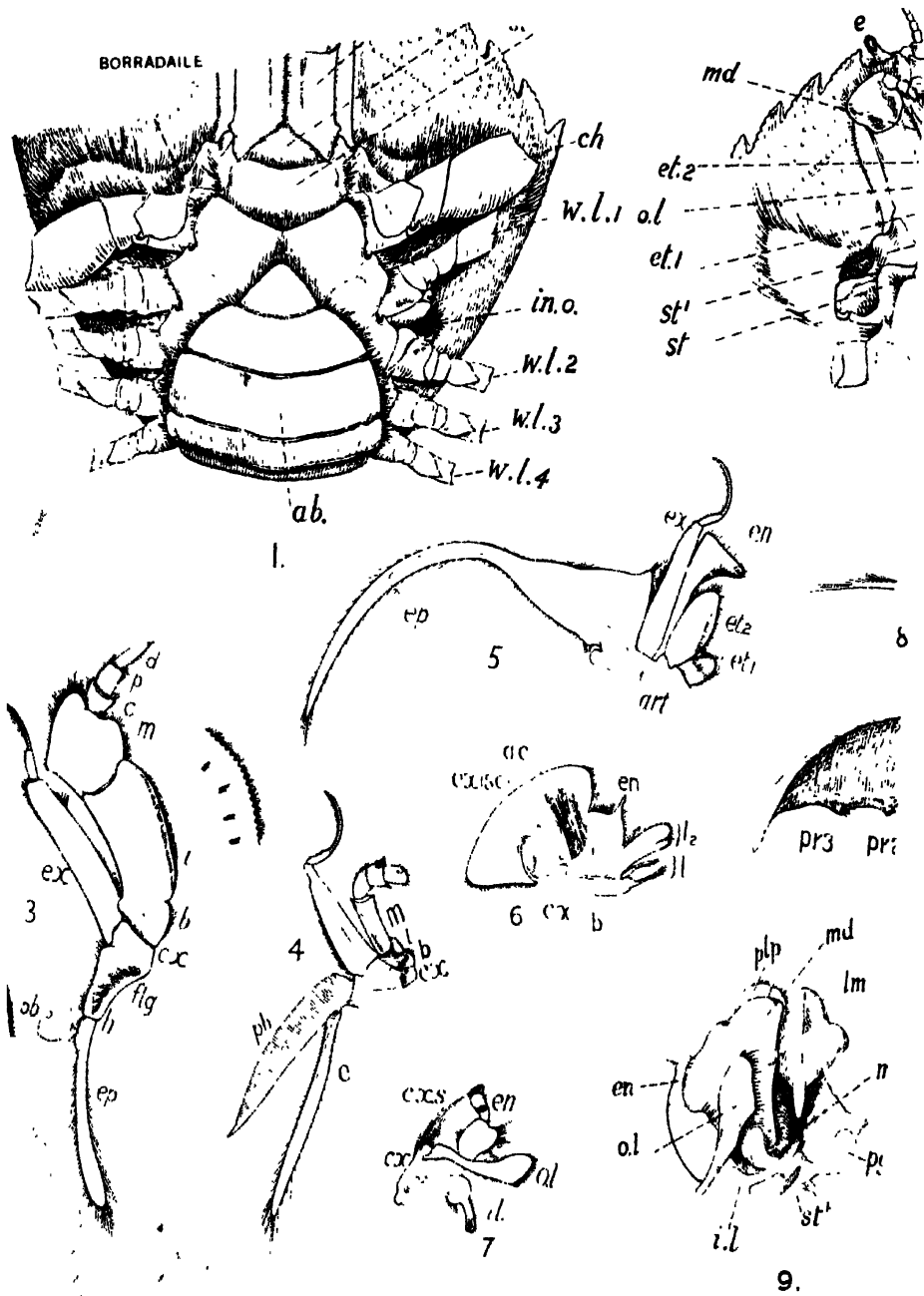
- Fig. 1. A ventral view of a female of the Shore Crab (*Carcinus maenas*). On the left side of the animal the first and second walking-legs have been parted, to expose the approach to the inhalent opening between them, and on the right side the cheliped has been turned back to reveal as much as possible of the flange on the coxa of the third maxilliped, by which the inhalent opening of Milne-Edwards is guarded.
- Fig. 2. The forepart of a similar view after the third maxillipeds have been divaricated, one of them cut short beyond its basis, and the chelipeds removed with the exception of their coxæ.
- Fig. 3. A ventral (posterior) view of the third maxilliped of the right side, removed from the body and flattened. The dotted line shows the normal position of the epipodite. The small drawing annexed shows a portion of the dorsal (anterior) surface of the ischium of the yellow appendage, enlarged.
- Fig. 4. A similar view of the second maxilliped of the right side.
- Fig. 5. A similar view of the first maxilliped of the right side.
- Fig. 6. A similar view of the maxilla (second maxilla) of the right side.
- Fig. 7. A similar view of the maxillule (first maxilla) of the right side.
- Fig. 8. A similar view of the mandible of the right side.
- Fig. 9. A view of the mouth and of the structures around it, after removal of all the paired appendages save the maxillule and mandible of the right side.
- Fig. 10. A diagram of a transverse section through the branchiostegite and the structures which underlie it at the level of the articulation of the first walking-leg.
- Fig. 11. A diagram of a longitudinal section through the branchial chamber of the left side. The podobranch of the second maxilliped is shown in perspective, and the position of the arthrobranchs of the third maxillipeds is indicated in dotted lines.
- Fig. 12. A view of the Crab from the left side after removal of the branchiostegite. Part of the inner roof of the gill-chamber remains, and is held back by a hook above the third walking-leg.
- Fig. 13. A view from within of a portion of the removed branchiostegite of the same side.
- Fig. 14. A view from below of the inhalent openings above the first and second walking-legs of the same side.
- Fig. 15. A view from above of the gill-chamber of the same side. The portions of the inner roof which have not been removed are held back by hooks.
- Fig. 19. Portions of hairs from the third maxilliped:—A, from the median band of the ischium; B, from the palp of the same limb; C, from the flagellum of the exopodite.

## PLATE 11.

- Fig. 16. A view similar to that in Fig. 15, after the removal of the greater part of the gills.
- Fig. 17. A similar view after complete removal of all the gills, save those of the second maxilliped, the third maxilliped being in the normal position.
- Fig. 18. A similar view with the third maxilliped divaricated from its fellow.





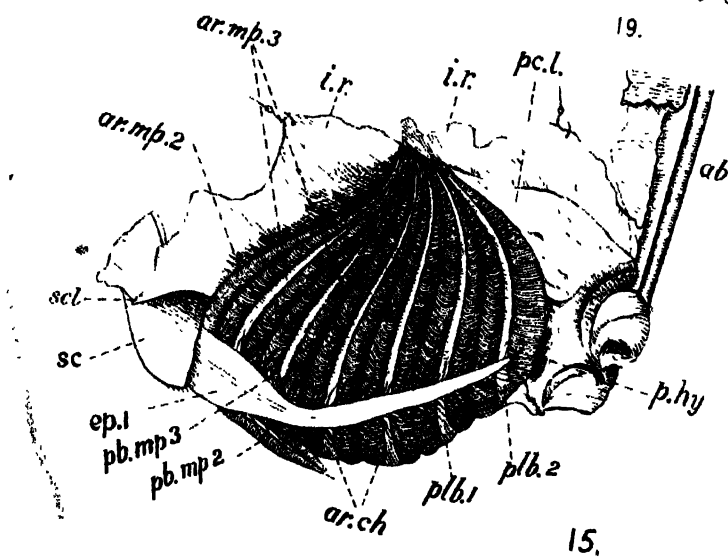
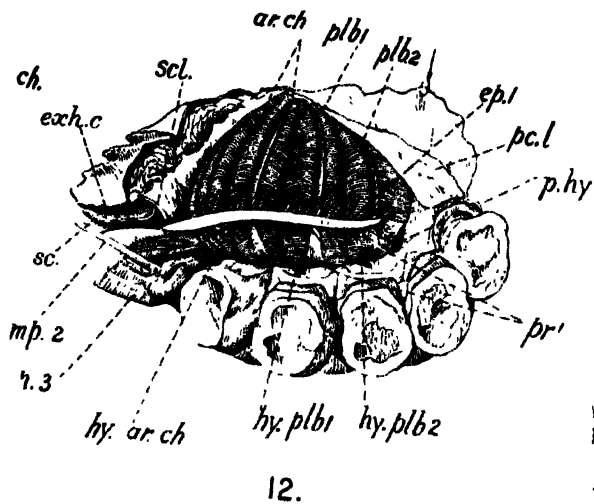
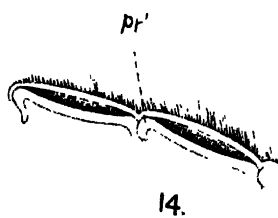
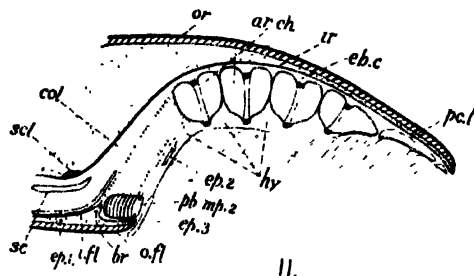


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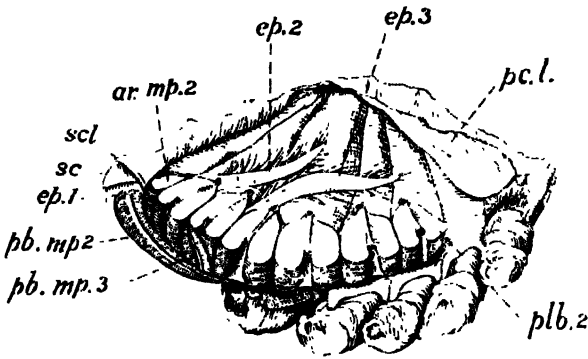


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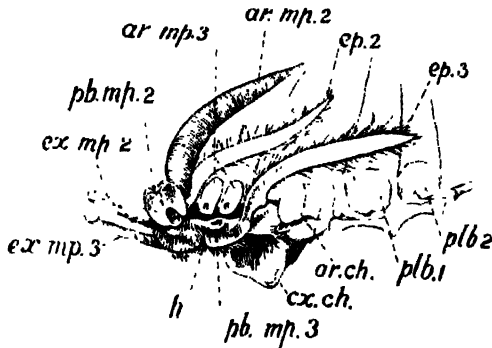
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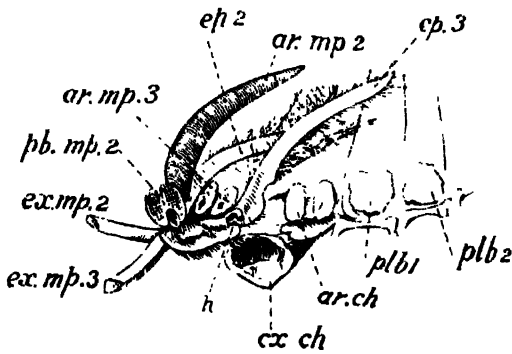




16.



17.



18.

MOUTHPARTS OF SHORE CRAB



The Wing-Venation of the Order Plecoptera or Mayflies. By R. J. TILLYARD, M.A., Sc.D. (Cantab.), D.Sc. (Sydney), F.L.S., C.M.Z.S., F.E.S., Entomologist and Chief of the Biological Department, Cawthron Institute, Nelson, N.Z.

(With 10 Text-figures.)

[Read 30th November, 1922.]

THE present paper is intended to be read in conjunction with the series of papers being prepared by me on the Wing-Venation of the Order Odonata or Dragonflies, the first of which has already been published (Tillyard, 1922), the remainder having been kept back to allow of the present results being considered first.

At the present time, considerable doubt appears to exist as to the true interpretation of the homologies of the wing-veins in Mayflies. This is not to be wondered at when we consider that Comstock and Needham originally offered one interpretation (1899), which became widely accepted, but that, following on Needham's discovery (1903) of the crossing-over of the supposed Rs in Anisopterous Dragonflies, Miss Anna Morgan (1912), working clearly under the influence of this discovery, offered a new interpretation bringing the venation of the Mayflies into line with that of the Dragonflies in this very important respect, although the evidence brought forward in her paper to support this view is admittedly of the slenderest kind. Space will not allow us to give here a full critical discussion of Miss Morgan's paper. It will only be necessary to make a single quotation from it, as follows (*l. c.* p. 98):—

"An actual connection between R and Rs trachea (in Mayflies) cannot be shown by constant structures. Moreover, Mayflies and Dragonflies are closely-allied groups, and their general tracheation is similar in many points. Furthermore, this condition of the radial sector trachea is exactly the same as that just described in the Damselflies, where there can be no doubt that such a crossing has taken place. It is, therefore, highly probable that the radial sector is present in Mayflies, and that both the sector trachea and the vein Rs have been stranded on  $M_1$ , and have left no positive trace of their origin."

On these very slender and debatable grounds, Miss Morgan proceeded to alter the homologies of the wing-veins in the Order. While recognising and admiring the painstaking work shown in her study of the tracheation and venation of so many little-known types, we have to confess that, like Prof. MacGillivray, under whom the work was done (*l. c.* p. 89), we "disagree with some of the interpretations . . . presented."

Now that I have shown the strong improbability that the supposed Rs of Needham in the Anisoptera is really not that vein (Tillyard, 1922), and definite proof is forthcoming that, in the Zygoptera, the supposed Rs never



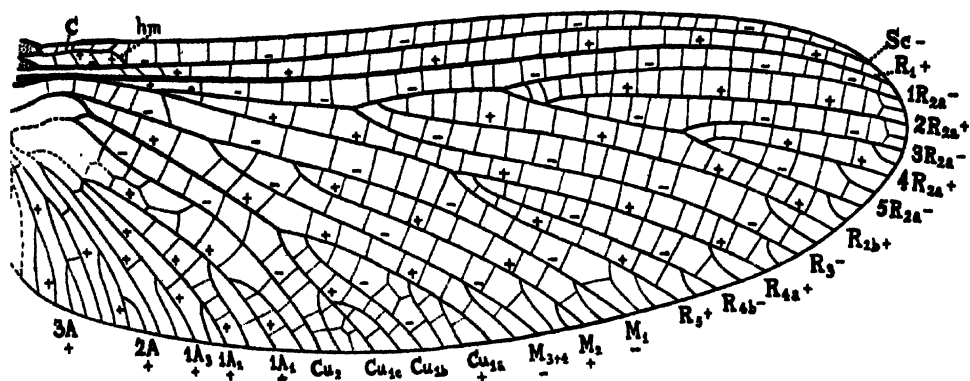
had any connection with R at all, and is most certainly not that vein, any system of homologies based on these results of Needham in the Odonata becomes so highly speculative in character as to cease to attract even those who may have originally accepted it. It is, therefore, necessary to enquire anew into the whole question of the homologies of the wing-veins of the Order. This I have attempted to do during the last three years. The results obtained appear to me to show, not only that the system proposed by Miss Morgan was incorrect, but that the original system proposed by Comstock and Needham (1899) was also wrong, and that the true interpretation of the homologies is one hitherto unsuspected in any quarter. These results, again, also support some startling new results obtained for the Odonata; and it is for that reason that the publication of the present paper is interpolated between the first and second papers of the series on that Order.

For the purpose of obtaining a really trustworthy result in an admittedly difficult problem, I have attempted to combine three methods of study, viz.: (1) the study of the Palæozoic Mayflies; (2) the study of the nymphal tracheation in archaic existing types; and (3) the application of the principles of convex and concave veins, both to fossil and recent forms. Good fortune favoured this plan. In the first place, when visiting New Zealand in 1919-20, Prof. C. Chilton, of Canterbury College, Christchurch, very kindly accompanied me on a visit to the Cass Biological Station, which is under his charge. Here we found abundant material of the larvæ of the archaic types of Siphuridæ for which New Zealand is famous. As all the necessary apparatus for dissections and microscopic study were at hand in the Station, I was able to make a thorough study of these larvæ on the spot. This produced a surprise, in that the tracheation was found to be almost complete in the various instars, and fairly easy of interpretation; whereas, in the Mayflies studied by Miss Morgan, the tracheation was both incomplete and irregular. Following on this discovery, during my visit to America in 1920, through the kindness of Prof. C. Schuchert, I studied the Lower Permian fossils left behind by Dr. Sellards in Yale University, and was surprised to find among them a very fine specimen of *Protereisma*, so beautifully preserved that it at once gave me the key to the whole venation of the Order, and, incidentally, supported the evidence given by the study of the larval tracheation. It then became clear to me that, if the significance of the alternation of convex and concave veins had been fully understood, and applied to the solution of this problem, the homologies would at once have become perfectly clear. In his paper on the Lower Permian Mayflies, Sellards (1907) entirely ignored this important point. Consequently, no help was to be obtained from his work by Miss Morgan, and she merely contents herself with copying his figures (1912, pl. 9, figs. 62-66), and attaching thereto the results obtained by her own researches.

Text-fig. 1a shows the hind-wing of a species of *Protereisma* with the homologies of the veins obtained by this new method of study. For

purposes of comparison the fore-wing of *Ameletus ornatus* is placed on p. 146 (text-fig. 1b). The corresponding notations of Comstock-Needham and Morgan are given in the accompanying table. In the second column the alternate convexity and concavity of these veins is indicated by the signs + and -.

TEXT-FIG. 1 a.



Hind-wing of *Protereisma* sp., Lower Permian of Kansas; the fore-wing is closely similar, but a little narrower at base, as shown in text-fig. 3.

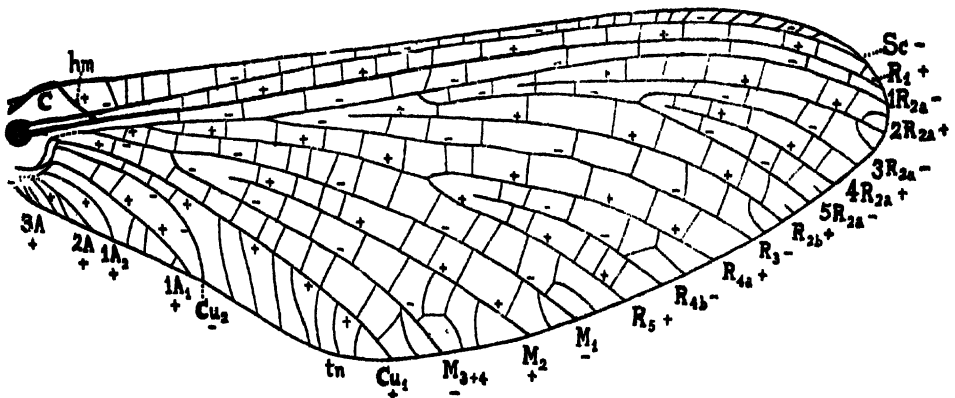
TABLE OF WING-VENATION OF MAYFLIES.

New Notation.	Sign.	Comstock-Needham Notation.	Morgan's Notation.
C	+	C	C
Sc	-	Sc	Sc
R <sub>1</sub>	+	R <sub>1</sub>	R <sub>1</sub>
1R <sub>2a</sub>	-	R <sub>2</sub>	M <sub>1</sub>
2R <sub>2a</sub>	+	(omitted)	(omitted)
3R <sub>2a</sub>	-	(omitted)	(omitted)
4R <sub>2a</sub>	+	(omitted)	(omitted)
5R <sub>2a</sub>	-	R <sub>3</sub>	R <sub>s</sub>
R <sub>2b</sub>	+	R <sub>4</sub>	Interpolated vein 1.
R <sub>3</sub>	-	R <sub>5</sub>	M <sub>2</sub>
R <sub>4a</sub>	+	M <sub>1</sub>	M <sub>3</sub>
R <sub>4b</sub>	-	M <sub>2</sub>	(omitted)
R <sub>5</sub>	+	M <sub>3</sub>	M <sub>4</sub>
M <sub>1</sub>	-	Cu <sub>1</sub>	Cu <sub>1</sub>
M <sub>2</sub>	+	Interpolated vein.	Interpolated vein.
M <sub>3+4</sub>	-	Cu <sub>2</sub>	Cu <sub>2</sub>
Cu <sub>1</sub>	+	1A	1A
Cu <sub>2</sub>	-	2A	2A
1A	+	3A	3A
2A	+	3A	3A
3A	+	3A	3A

It will be noticed that no less than five branches of  $R_{2a}$  are indicated in the new notation. An explanation of this will be found in the argument on page 148 concerning the nature of triads.

The results obtained by the three methods of study, already mentioned, support one another, except that in the case of the study of the larval tracheation a certain amount of variation is normally present. I have therefore presented the argument based on the Convexity and Concavity of the veins first, followed by that deduced from the study of these conditions as noted in the fossil *Protereisma*, and have kept for the last place the results obtained from the larval tracheæ. In dealing with these last, the alternative interpretations given in the table on p. 145 will be considered, and reasons given for rejecting them.

TEXT-FIG. 16.



Fore-wing of *Ameletus ornatus* (Eaton), Recent, for comparison with text-fig. 1a. *tn*, tornus. Lettering as on p. 162.

#### CONVEX AND CONCAVE WINGS.

In all generalised insects, we are able to distinguish the presence of two kinds of veins on the wings, viz. those which occupy the summits of ridges, commonly called *convex veins* (indicated by a *plus* sign), and those which lie in the bottoms of grooves or hollows, commonly called *concave veins* (indicated by a *minus* sign). In the ideal archetypic wing, convex and concave veins follow one another alternately across the main portion of the wing, Sc being -,  $R_1$  and its sector +, M -, the vein commonly called  $Cu_1$  +, and  $Cu_2$  -. This last is always to be distinguished by lying either in or very closely anterior to the deep *anal furrow*, which separates off the *clavus* or *anal area* from the rest of the wing. The clavus itself is a *wholly convex area*, and carries only convex veins, viz. the three anal veins 1A, 2A, and 3A. In an ideal forked vein, both branches of the fork keep the same condition of convexity or concavity as the main stem; but the alternation of ridge and

hollow is preserved, in the case of areas broad enough, by the development of intermediate branches which take the opposite condition to the two branches which they separate. These have been considered as *interpolated veins* in the Mayflies; i.e., they have been supposed to develop from the margin of the wings inwards, and not to be true branches of the main veins at all. A study of the fossil Mayflies shows, however, that originally there were no interpolated veins in this Order at all, and that the discontinuity of these veins has been brought about actually by absorption of the basal connections with the veins of which they are true branches.

The primitive system of branching which is shown almost to perfection in the Permian Mayflies is the type which we may conveniently term the *triad*. This can be understood from text-fig. 2. *V* is a convex vein which divides

TEXT-FIG. 2.

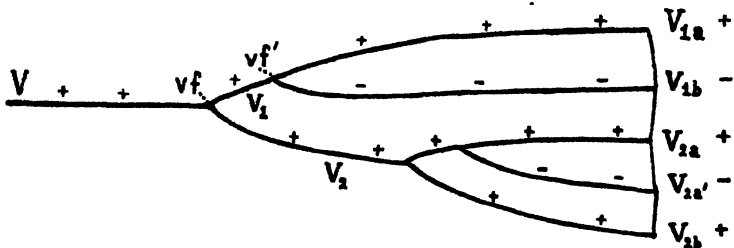


Diagram of the triadic system of branching of main veins. For explanation, see text.

at its primary fork *rf* into two equally convex branches  $V_1$  and  $V_2$ . In the diverging angle between these two, a concave vein arises from either  $V_1$  or  $V_2$ , its point of origin being not far distad from *rf*; this secondary fork is termed *rf'*. In the illustration before us, the concave vein is made to arise from  $V_1$ , so that the two branches of this vein become  $V_{1a}$  (+),  $V_{1b}$  (-), and  $V_2$  (+). If, instead of being a convex vein, *V* were a concave vein, then the two branches  $V_1$  and  $V_2$  would be concave, and the intermediate vein  $V_{1b}$  would be convex. The two cases can be distinguished by calling the triad developed from an originally convex vein a *positive triad*, that from an originally concave vein a *negative triad*.

Further branching may take place from any one of the three veins of a triad, and usually consists of the development of further triads. In text-fig. 2, a further triad is seen developed from  $V_2$ , viz. the positive triad  $V_{2a}$  (+),  $V_{2a'}$  (-), and  $V_{2b}$  (+). If a triad had been developed from  $V_{1b}$ , it would have been a *negative triad*, and the notation used would have been  $1V_{1b}$  (-),  $2V_{1b}$  (+), and  $3V_{1b}$  (-); this notation was chosen to avoid duplication of suffixes.

We can now see what has happened to the radius in *Protereisma*. This vein is convex, and divides first of all into a positive triad,  $R_1$  (+),  $R_{2+3}$  (-), and  $R_{4+5}$  (+). The negative member of this group,  $R_{2+3}$ , next develops a

negative triad, viz.  $R_{2a}(-)$ ,  $R_{2b}(+)$ , and  $R_3(-)$ . The second and third members of this triad remain unbranched to the margin; but the first,  $R_{2a}$ , develops another negative triad, from the third branch of which a further negative triad is also developed. To save complications in the notation, I have named the five veins developed on the wing-margin by these two latter triads  $1R_{2a}$ ,  $2R_{2a}$ ,  $3R_{2a}$ ,  $4R_{2a}$  and  $5R_{2a}$ ; it will be noticed that they are alternately concave and convex.

The triad system, as will be clearly seen, always results in the formation of alternately convex and concave veins along the wing-margin. There is a large body of evidence to show that, apart from the Mayflies, this system was the original system of branching of the veins in the insect wing. Consideration of this evidence is beyond the scope of this paper, but attention is drawn to it in the hope that students of other Orders will attempt to recognise the remains of triads in the wings before them. As examples of archaic triads, we may take the universally recognised primitive set of three branches of  $R$ , viz.,  $R_1$ ,  $R_{2+3}$ ,  $R_{4+5}$ , which is formed from an original positive triad with the intermediate vein developed from the lower branch  $R_3$ . A similar archaic triad appears also to have developed from  $M$ , viz.  $M_1(-)$ ,  $M_2(+)$ , and  $M_{3+4}(-)$ , as shown in *Protereisma*, though this triad often appears in other insects as  $M_{1+2}(-)$ ,  $M_3(+)$ , and  $M_4(-)$ , owing to a difference in the position of the origin of the intermediate vein. It will readily be seen how easily a pectinate series can be developed from the triadic system; an example of this can be seen in the vein  $Cu_1$  in *Protereisma*. Simple dichotomies, on the other hand, may be explained by either the non-development or suppression of the middle member of a triad, as in the case of the secondary branches of  $R$ s in most insects.

We now pass from the consideration of the triad to the application of the rule of alternate convexity and concavity of veins as it affects the problem of the elucidation of the homologies of the wing-veins in an archaic Mayfly such as *Protereisma* (text-figs. 1, 3). The general rules applicable to all except very highly-specialised wing-types may be stated as follows:—

(1) Two strongly convex veins can always be recognised lying between the costal margin and the anal furrow, viz.,  $R_1$  and  $Cu_1$ .

(2) The concave vein lying between  $R_1$  and the costal margin is  $Sc$ .

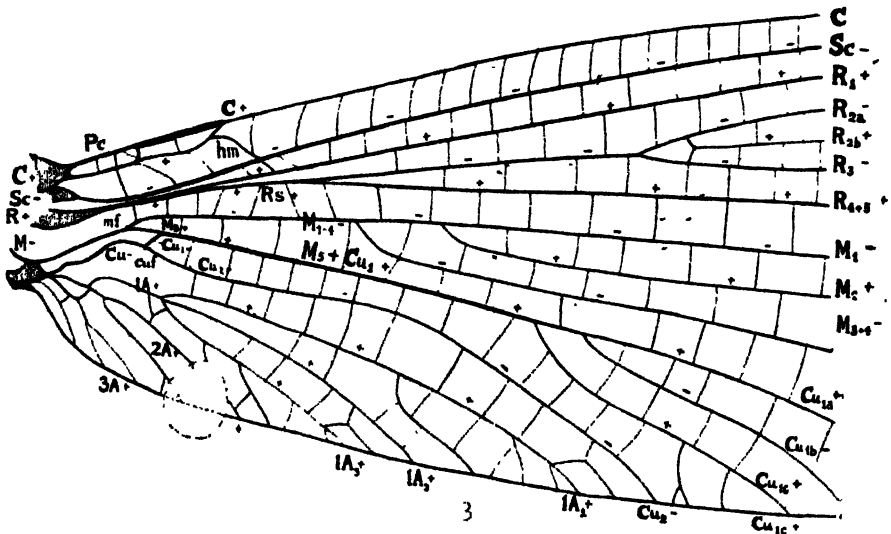
(3)  $M$  is a weakly concave vein lying between two ridges of  $R_1$  and  $Cu_1$ . In many archaic types it gives off a posterior branch close to the base, which joins with  $Cu_1$ , thus forming the *cubito-median Y-vein*, the main stem of which is properly denoted by  $M_3 + Cu_1$ , though usually called simply  $Cu_1$ . If this Y-vein can be recognised, any doubts as to the limits of  $M$  and  $R$ s should be finally removed.

(4) The vein lying either in or slightly anterior to the anal furrow is the *vena dividens*,  $Cu_2$ .

(5) The clavus or anal area is a wholly convex area, and may carry from one to three convex anal veins, any of which may be branched or simple.

Applying these rules to a well-preserved specimen of *Protereisma*, such as the one figured in text-fig. 3, which Prof. Schuchert kindly allowed me to keep for study during the last two years, the archaic condition of the wing-venation is clearly shown in that the application of all five of the above rules can be made without any doubt or hesitation. The high ridge of  $R_1$  can be found at once with the concave vein  $Sc$  lying anterior to it. At the base of the wing there is developed a short convex vein between  $Sc$  and the costal border. This must be considered as a true primitive costal vein, ( $C$ ), not a basal branch of  $Sc$ , since it is convex and not concave. Sellards (1907) has already shown how it forms a brace for the costal border, and has its homologue in existing Mayflies.

TEXT-FIG. 3.



Basal portion of fore-wing of *Protereisma* sp., Lower Permian of Kansas, considerably enlarged to show details of venation. Note the cubito-median Y-vein having  $M_1$  as upper arm,  $Cu_1$  as lower arm, and  $M_1 + Cu_1$  as main stem. For lettering, see p. 162.

We should next set about determining ( $Cu_1$ ), the anal furrow and the clavus, keeping the consideration of  $M$  and  $Rs$  until the last, as it is the limits of these veins which have been the chief trouble in the past. Again returning to our specimen of *Protereisma*, we find that the only vein which satisfies the conditions for  $Cu_1$  is that which has previously been called  $1A$ , and that its concave branch  $Cu_2$  can be clearly seen running in the anal furrow with a characteristic curve basally, and separating off from the rest of the wing a small, but quite distinct, convex clavus on which only convex veins are

present. In order to test this conclusion, we next look for the cubito-median Y-vein, and find that it is present quite close to the base of the wing in the very characteristic form shown in text-fig. 3. This definitely determines the correct homology of the vein  $M_3 + Cu_1$ , and enables us to pick up at once the true median above it, viz. the concave vein which had previously been called  $Cu_1$ , in spite of the fact that it is not convex. We thus find that  $M$  is a three-branched vein, excluding  $M_3$ , of triadic type, just as it is in so many of the Palæodictyoptera themselves.

We now have only the limits of  $Rs$  to consider. The whole of the many-branched vein which had previously been considered to be formed of  $Rs$  and  $M$ , combined by basal fusion, is now seen to belong to  $Rs$  alone. It arises from  $R_1$  near the base, and its short basal piece is convex. It then branches into a concave upper branch ( $R_{2+3}$ ) and a convex lower one ( $R_{1+5}$ ); and thus, as already indicated above, it makes with  $R_1$  a true positive triad. The numerous branchings of  $Rs$  shown in *Protereisma* need not be a cause of wonder, since they are paralleled in quite a number of Palæodictyopterous types.

In text-figs. 1 and 3, it should be noted that, excluding the clavus, on which all the veins are convex, the whole of the veins reaching the wing-margin are placed alternately convex and concave. The complete notation for the wing of *Protereisma* has been already given in the table on p. 145.

#### COMPARISON OF THE VENATIONS OF FOSSIL AND RECENT MAYFLIES.

The next step is to make a careful comparison between the venation of fossil Mayflies and the more archaic representatives of existing types. For this purpose, I have chosen the wings of *Ameletus ornatus*, family Siphuridae; not because I believe it to be the most archaic of existing types, but because it is archaic enough for our purpose, and happens to be the species on which most of the studies of larval wing-tracheation were carried out.

Comparing the wings of *Protereisma* (text-figs. 1a, 3) with the fore-wing of *Ameletus* (text-figs. 1b, 4), the first thing we notice is the change in the general shape of the wing. That of *Protereisma* is of the archaic elongate oval form seen in most of the Palæodictyoptera and in the fore-wings of *Perlaria*, in which no definite tornus and termen are developed, but only a single continuously curved posterior margin from base to apex. In most recent Mayflies, *Ameletus* included, a definite *tornus* (*tn*) is to be recognised; the angle of the tornus divides the original posterior margin into a shorter basal part, to which the term *posterior margin* is still applied (called the *dorsum* in Lepidoptera, but the term is inapplicable to Mayflies, which do not fold their wings over their body in a roof-like manner), and a much longer distal part, called the *termen* or *distal margin*. The result of this is that the wing is now no longer of the primitive elongate oval shape, but

definitely triangular, the three angles being the base, the apex, and the tornus. In the evolution of this shape of wing there is a definite reduction of the areas served by the cubitus and anal veins, and a definite increase in the area served by the media and radial sector. Consequently, if Comstock and Needham's theory of interpolated veins is justified, we should certainly expect to find a number of them developed along the termen in *Ameletus*. At first sight, this appears to have happened, since we can find at once no less than five long veins, viz.  $2R_{2+3}$ ,  $4R_{2+3}$ ,  $R_{4+5}$ , and  $M_2$ , which are not connected basally with their adjacent main veins. On the evidence of recent Mayflies alone, Needham's conclusions were perhaps warranted. But when we come to compare the venation of *Ameletus* with the fossil *Protereisma*, we find that every one of these veins corresponds exactly with a true branch of a main vein present in the fossil: and, further, the total number of veins present in *Ameletus*, and their alternate convexity and concavity, agrees exactly with the conditions in *Protereisma*. I have therefore no hesitation in assigning to the veins in the fore-wing of *Ameletus* the same names as I have already given to their homologues in *Protereisma*.

In the section dealing with larval wing-tracheation, it will be shown that disconnection of the base of any branch vein is correlated with loss of its precedent trachea in the larval wing, and may well be a direct result of this larval condition.

By comparing the wings of *Ameletus* and *Protereisma*, we are now able to see that the lengthening of the termen has taken place chiefly in the region served by  $R_{4+5}$  and  $M$ , the branches of these veins standing considerably further apart in *Ameletus* than in the fossil, whereas the area served by  $R_{2+3}$  has altered very little.

Turning our attention to  $Cu_1$ , we note that this remains a strongly convex vein, but its original triadic system of branching has been changed to a simple pectinate series, though the number of branches, seven in all, remains the same, the branches still being alternately convex and concave. Though superficially striking, this change is really a very slight one, consisting only of a movement basad, on to the main stem, of the triad called  $Cu_1$ , in text-figs. 1a, 3.

The greatest changes that have taken place in the evolution of the existing type of Mayfly wing are those in the basal region of the wing. For these, we must refer to the enlarged basal area of *Ameletus* shown in text-fig. 4, and this must be compared with the basal portion of the wing of *Protereisma* in text-fig. 3. Here we note the following changes:—

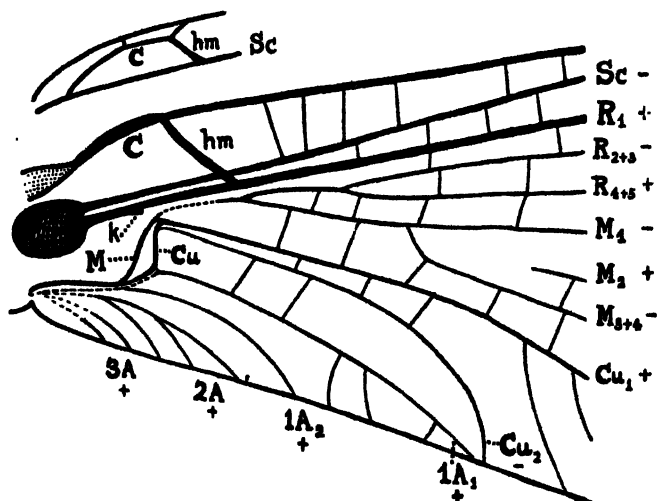
(1) The separate costal vein  $C$  of the fossil has become fused with the costal margin, forming a thickened basal margin; only its posterior distal branch,  $hm$ , remains free, and forms the strong oblique brace,  $hm$ , in *Ameletus* and all recent Mayflies. The intermediate stage in this evolutionary process is well seen in the Jurassic Mayflies, the condition in *Mesephemera cellulosa* (Hagen) being shown in text-fig. 4, upper figure.



(2) M has become fused basally for a short distance with Rs, the basal stem of the two veins becoming obsolescent, but actually showing a weak connection with M only, while the lost origin of Rs is shown by a very definite stump projecting from  $R_1$  close to the base. In some recent Mayflies, however, Rs remains separate from M, and is attached tangentially to  $R_1$  just beneath *hm*. Both conditions may be regarded as specialisations involving the abortion of the original basal piece of Rs.

(3) The basal portions of M and Cu, before the first forkings of these veins, run close together as in *Protereisma*, but both of them turn upwards almost transversely across the wing. At the upper end of this bent portion is the formation which I have called the cubito-median Y-vein, so greatly

TEXT-FIG. 4.



Basal portion of fore-wing of *Ameletus ornatus* (Eaton), Recent, considerably enlarged to show details of venation. *k*, stump of Rs. Above, costal vein and humeral brace (*hm*) in *Mesephemera cellulosa* (Ilagen), Upper Jurassic of Solenhofen. For lettering, see p. 162.

reduced from its original conditions (as seen in *Protereisma*) that it can only just be made out in text-fig. 4. At this point, Cu forks, and its two branches turn at right angles to its former course and run outwards about parallel to the posterior border of the wing. Cu<sub>2</sub> remains, as in the fossil, a strongly-curved vein concave to the posterior border; but the shortening of its length has brought with it a definite increase of curvature, so that the weak sigmoid curve which this vein shows in *Protereisma* becomes replaced by a single strong arch, concave to the posterior border. Other recent Mayflies, such as *Ephemera*, have the original sigmoid curve intensified, but the vein itself greatly reduced in length, and the clavus almost completely obliterated.

(4) The anal area, or clavus, in greatly reduced size, being about one-fifth of the total wing-length in *Ameletus*, as compared with about one-third in *Protereisma*. The number of branches of the anal veins are correspondingly reduced, those of 1A to two definite branches, while 2A and 3A are only indicated by short, weakly-formed veins, as shown in text-fig. 4.

(5) The articulation of the wing, situated at the origin of Sc and R, becomes greatly strengthened by the formation of a high ovoid callus (text-fig. 4). It appears to be the growth of this callus which has forced the basal portions of M and Cu below it into their peculiar curved positions. In some recent Mayflies of higher type than *Ameletus*, these curved basal parts of M and Cu become strengthened and partially fused together; uniting with the bases of the anal vein also, they form an upwardly-curving arch convex to the posterior border, from which all the branches of Cu and A take their rise.

We thus see that, in the archaic family Siphuridæ, as represented by *Ameletus*, the correspondence with the Lower Permian fossil Mayflies is exceedingly close, and the homologies of the veins perfectly clear. This, of course, refers to the fore-wing only. The hind-wing, which has undergone great reduction since Jurassic times, will be dealt with after the tracheation of the larval fore-wing has been considered.

#### TRACHEATION OF THE LARVAL WINGS.

The study of the tracheation of the larval wings in New Zealand genera of the family Siphuridæ was carried out chiefly, as already stated, in the Cass Biological Station. Some material was also obtained around Wellington during my stay with Mr. Harold Hamilton, of the Dominion Museum, and the dissections of these were carried out at his home in Karori. I wish here to thank Prof. Chilton and Mr. Hamilton for the facilities they afforded me for carrying out this work.

The material studied consisted of numerous larvæ of the following species:—*Oniscigaster distans* Eaton, *Coloburiscus humeralis* (Walk.), *Ameletus ornatus* (Eaton), and *Ameletus perscitus* Eaton. The larvæ of the first and last of these were very abundant at Cass, and provided the bulk of the dissections. The number of instars is not known for any of these larvæ, but the wing-sheaths can be dissected out for at least five instars, showing comparative stages of growth from a tiny triangular bud up to a considerably elongated flap. For comparative purposes, I have designated the youngest of these last five instars as the  $n$ th instar, viz. that in which the wing-buds are very small flaps, capable of being dissected off with very fine scissors if great care is exercised. The following instars will be termed the  $(n+1)$ th,  $(n+2)$ th,  $(n+3)$ th,  $(n+4)$ th respectively, the  $(n+4)$ th being the last larval instar. In order to avoid too many figures, I shall give

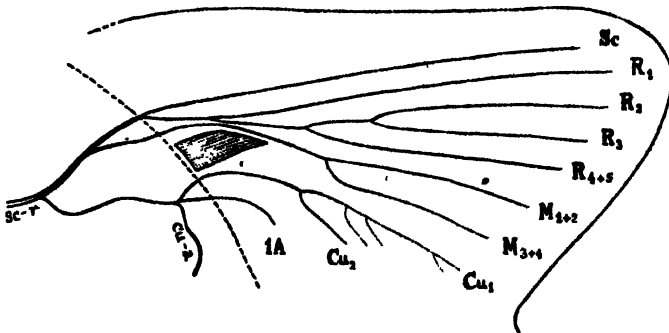
here only a series of drawings which I made from the wing-sheaths of *Ameletus ornatus*, a larva which has fairly transparent wings, is easy to dissect, and in which the tracheæ can be followed without any trouble. Characters in which the other larvæ differed from this will be noted below.

The first point to be noticed is that the larval wing, in this Order, is soldered to the thorax over a considerable portion of its basal area.

The free distal portion of the wing is that which lies to the right of the dotted line in text-figs. 5-9. Great care is necessary, in dissection, to remove sufficient of the soldered basal part to ensure that the bases of the wing-tracheæ, and their connections, are not severed or damaged in the operation.

Just distad of the middle of the line marking the junction of the flap of the wing with the thorax, there is always present a somewhat triangular patch of hard chitin, shown shaded in all the figures. It at first separates the subcosto-radial group of tracheæ, including M, from the cubito-anal group, as shown in text-fig. 5 for the *n*th instar. But, in the next instar, it

TEXT-FIG. 5.



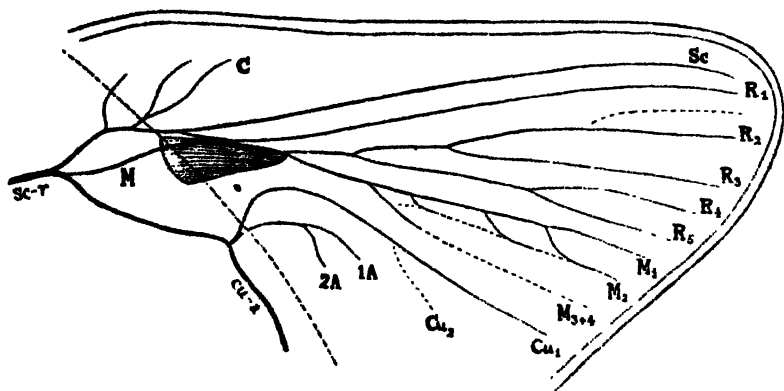
*Ameletus ornatus* (Eaton). Tracheation of fore-wing in *n*th larval instar.

For lettering, see p. 162. ( $\times 97$ .)

moves forward a little, so as to overlie part of the base of M; and finally, in the last two instars, it comes to overlie the wholly or partially fused bases of R and M. From its final position in the last instar, it seems to me that this hard piece of chitin represents the large callus of the imaginal wing; its position in relation to the thorax is probably constant, its apparent movement forward being probably due to changes in the actual positions of the wing-tracheæ. The chief point of interest appears to me to be that it certainly does cause trachea M to run closer up to R than it naturally would if this callus were absent. Consequently, it may well be one of the factors which helped to bring about the fusion of M with Rs basally, as we find it in the majority of larval wings in the last four instars (text-figs. 6-8).

Text-fig. 5 shows a typical fore-wing of *Ameletus ornatus* in the  $n$ th larval instar. There is no costal trachea visible. The alar trunk connecting the subcosto-radial with the cubito-anal group of tracheæ is complete, though of small calibre, and the two groups are widely separated. Instead of coming off separately from the alar trunk, the tracheæ Sc, R, and M arise as separate branches from a single trachea of large calibre. Rs branches, as a simple triad, into  $R_2$ ,  $R_3$ , and  $R_{4+5}$ . Trachea M arches gently in front of the callus already mentioned, and thus comes very close up to Rs just where it comes off from  $R_1$ . Most of the larvæ examined in this instar show exactly the condition given in text-fig. 5; but I found one larva in which trachea M had already captured trachea Rs at its base. This condition becomes the usual one in the following instars. M is only two-branched, as in the Order Perlaria. The tracheæ of the cubito-anal group are very fine in calibre; but I could distinctly make out  $Cu_1$  and 1A in all the larvæ examined, and could see  $Cu_2$  in most of them. In following instars, no trachea is usually visible in  $Cu_2$ , though I found it quite well developed in a fine larval wing of the penultimate or  $(n+3)$ th instar shown in text-fig. 8.

TEXT-FIG. 6.



*Ameletus ornatus* (Eaton). Tracheation of fore-wing in  $(n+1)$ th larval instar.  
For lettering, see p. 102. ( $\times 87$ .)

Passing on to the next, or  $(n+1)$ th instar (text-fig. 6), we note that the callus has now come to overlie the base of M, and in the great majority of wings examined, trachea M has captured trachea Rs at its point of nearest approach basally. I have notes of a few exceptions, chiefly in the genus *Oniscigaster*, in which, both in this and the following instars, any of the following conditions may happen to occur:—

(1) Tracheæ Sc, R, Rs, and M all come off in a bunch as separate tracheæ from a single point on the alar trunk.

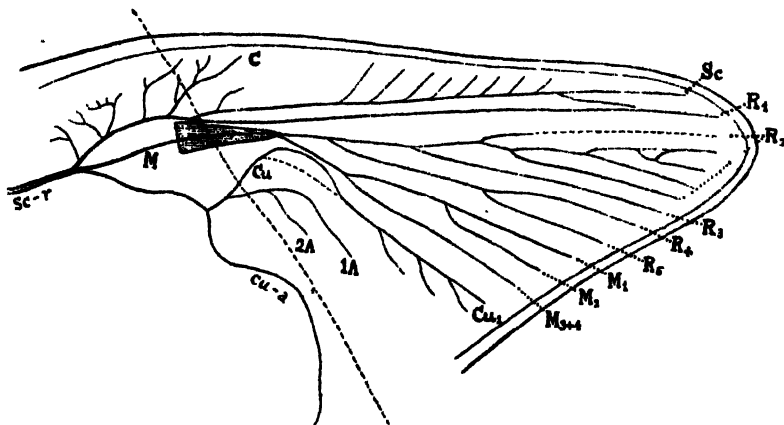
(2) R arises from Sc, but Rs and M arise close together from a point on the alar trunk a little below them.

(3)  $R_s$  and  $M$  are slightly separated basally, but come together so as to be almost indistinguishable while passing the callus, and then separate distally.

(4)  $Sc$  arises by itself from the alar trunk : considerably further down, a group of three separate tracheæ,  $R_1$ ,  $R_s$ , and  $M$ , arise close together.

All the above conditions are occasional variants only from the dominant condition, which is that shown in text-fig. 6. It should be noted that trachea  $M$ , in this instar, usually arises quite separately from trachea  $Sc + R_1$ , and its course basally from alar trunk to callus diverges widely from that of the latter. The number of tracheæ developed from  $R_s$  is increased to four by the forking of  $R_{4+5}$ , and there is an indication of the addition of an anterior branch to  $R_2$  in the form of a pale band, which never, at any time, as far as I could see, develops more than the inerst basal rudiment of a trachea, and usually possesses none at all. The number of branches of  $M$

TEXT-FIG. 7.



*Ameletus ornatus* (Eaton). Tracheation of fore-wing in  $(n+2)$ th or antepenultimate larval instar. For lettering, see p. 162. ( $\times 41$ .)

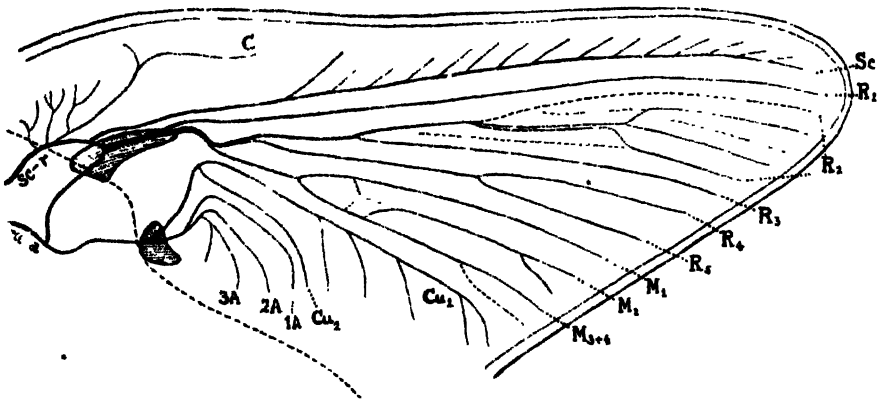
is also increased to three by formation of the triad  $M_1$ ,  $M_2$ ,  $M_{3+4}$ ; but the tracheal supply of the middle branch  $M_2$  is quite irregular, and varies greatly in the different larvæ examined. A separate costal trachea appears as a short basal anterior branch from  $Sc$ . The alar trunk continues complete, and of fair calibre.

Passing next to the  $(n+2)$ th or antepenultimate instar (text-fig. 7), we find the conditions not very different from those indicated for the previous instar, except for the presence of additional branches of  $R_s$ , which now number five in all, and the establishment of the triad  $M_1$ ,  $M_2$ ,  $M_{3+4}$  on a firm basis, with a single trachea supplying  $M_2$ , as shown. In text-fig. 7, I show a curious condition of trachea  $Cu_1$  near the base. The course of the vein  $Cu_1$  is indicated by the dotted line, but the trachea arches up out of its normal course, and passes close under  $M$ . I have seen this condition several times,

not only with  $Cu_1$ , but in other parts of the larval wing. It seems to indicate a certain amount of instability in the tracheation, and may possibly be the stage precedent to a more complete breaking down of the tracheal supply, as exhibited in many of the forms studied by Miss Morgan.

Text-fig. 8 shows the tracheation of the fore-wing in the  $(n+3)$ th or penultimate instar. In this stage, R, Rs, and M generally appear to arise as a single thickened trachea from the alar trunk, at a point somewhat removed from the origin of Sc, and beneath the callus. By careful manipulation, this apparently single trachea can be separated into its component parts, when it will be seen that it is in reality three separate tracheae arising from almost the same point. In some specimens, however,  $R_1$  may still be found arising as a branch of Sc, while Rs and M arise as a single trachea well below it. I think the varying conditions seen in the later

TEXT-FIG. 8.



*Ameletus ornatus* (Eaton). Tracheation of fore-wing in  $(n+3)$ th or penultimate larval instar. For lettering, see p. 162. ( $\times 48$ .)

instars are almost wholly due to the presence of the callus, one or more of the original tracheae taking a devious course to avoid passing under it, or possibly becoming displaced at ecdysis by the pressure of the harder mass of chitin.

In this instar, the number of branches of  $R_2$  is still five, and the most anterior of these never has any tracheal supply except a mere rudiment. Various irregularities may be noted. In the specimen figured, the trachea which usually supplies the most posterior branch of  $R_2$  arises alongside the trachea belonging to the branch above, and runs with it to about half its length, when it turns downwards and supplies the course of the most posterior branch for its distal half only. The trachea supplying  $M_2$  sometimes arises from  $M_{3+4}$ .  $Cu_2$  possesses a complete trachea in this specimen; but in the majority of wings examined, it either has no trachea or a mere rudiment. These are all individual variations in the tracheation, and

are of no significance except to indicate the essential variability of the tracheation in many of its details.

In this instar, the line of fusion of the wing-sheath with the thorax ceases to be straight, and shows a definite convex bulging between the subcosto-radial and cubito-anal groups of tracheæ. The alar trunk is still complete, but thrown into a strong loop. The large anterior callus already noted in previous instars now appears in close contact with the axillary area of the thorax, this position corresponding with that in the imaginal wing, where the callus articulates with the axillary process of the thorax. A new structure is apparent in the cubito-anal region, viz. a smaller, somewhat reniform, posterior thickened patch, shown shaded in text-fig. 8. This corresponds with the opaque and somewhat thickened anal area at the base of the imaginal wing; but it never becomes a true callus, *i.e.* it does not articulate with an axillary process from the thorax.

The last or  $(n+4)$ th instar differs from the previous one in the much larger size of the wing-sheaths, the strong development of the anterior callus, the very clear indication of the whole of the imaginal venation, including all the cross-veins and veinlets, and the presence of all six branches of  $R_2$ . In this instar, the tracheation is not easy to follow, owing to the strong pigment bands of the imaginal venation overlying it. As the general tracheation scheme is closely similar to that of the previous instar, and the same individual variations are equally apparent, it has not appeared necessary to me to figure it. One point of interest needs to be mentioned, viz. that I only succeeded in finding the complete alar trunk in one specimen of *Oniscigaster distans*. In all the others examined, the basal portion *cu-a* was missing, and the single trachea which gives origin to Cu and the anal veins appeared to arise from the same trunk as the other tracheæ above it. This is exactly the condition shown in Miss Morgan's figures (1912, pls. 5-7). Thus it will be seen that, if she had studied other instars as well as the last, she would not have fallen into the error of failing to homologise correctly the cubital tracheæ and veins, which it is quite evident she has done.

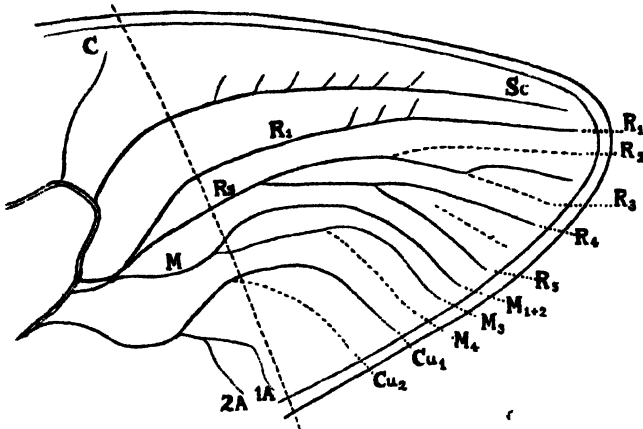
The above discussion applies to the fore-wing only. As the hind-wing is greatly reduced in size in all recent Mayflies, and differs very greatly from that of the Permian Mayflies, as well as from the fore-wing of recent forms, I have thought it best to summarise the evidence for its venational homologies in a separate section.

#### THE HIND-WING.

The dissection of the small hind wing-sheath of a Mayfly nymph is not easy, and I only succeeded in getting good preparations from the last two instars. Text-fig. 9 shows the tracheation in the hind-wing of *Ameletus ornatus*, penultimate instar. The alar trunk is complete, but there are no signs of a callus. The line of fusion with the thorax lies well out beyond the origins of the wing-tracheæ, as shown by the dotted line in the figure.

There is a separate costal trachea C, lying far above Sc; the latter trachea lies far above the group of R and M, which arise close together well down towards the cubito-anal group. Rs arises from R very close to the point

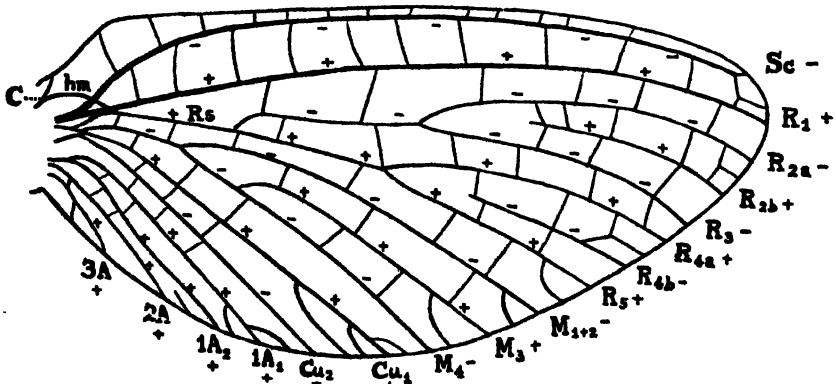
TEXT-FIG. 9.



*Ameletus ornatus* (Eaton). Tracheation of hind-wing in  $(n+3)$ th or penultimate larval instar. For lettering, see p. 162. ( $\times 87$ .)

where M curves slightly upwards, so as to come very close to it. Rs divides into two branches,  $R_{2+3}$  and  $R_{4+5}$ , each of which gives rise to a simple triad with incomplete tracheation. The middle branch of the triad of  $R_{2+3}$  is supplied by the trachea  $R_3$ , but  $R_2$  and the distal part of  $R_3$  have no tracheae. The two outer branches of the triad of  $R_{4+5}$  have their tracheae present, but

TEXT-FIG. 10.



*Ameletus ornatus* (Eaton). Venation of hind-wing. For lettering, see p. 162. ( $\times 16$ .)

the middle branch has none. M gives rise to a simple triad in which the trachea supplying  $M_{3+4}$  switches up into the middle branch distally, leaving the distal half of  $M_4$  without a trachea.  $Cu_2$  has no trachea.



In interpreting the above scheme, we must compare the imaginal venation shown in text-fig. 10 with the tracheation shown in text-fig. 9. There can then be no doubt as to the correct homologies of the main veins. Two points only are open to doubt. Firstly, what is the correct notation for the middle branch of the triad of  $R_{2+3}$ ? This appears to be a branch of  $R_2$ . But in the penultimate instar of *Oniscigaster distans*, I find the trachea  $R_2$  supplying this branch. I therefore conclude that the tracheation is variable, and give preference to the notation  $R_{2b}$  for this vein. This is done because, in the fore-wings of recent Mayflies, and also in both wings of the fossil *Protereisma*,  $R_2$  is an unbranched vein. Secondly, what is the correct notation for the middle branch of the triad of  $M$ ? In this case, both in the larva of *Oniscigaster distans* and in the one figured, the trachea supplying it comes from  $M_{2+4}$ . In addition to this, the vein itself, in the imaginal wing, arises from  $M_{2+4}$  as a definite branch. All the evidence, then, points to the correct notation for this vein being  $M_3$ , the other members of the triad being  $M_{1+2}$  and  $M_4$ . In this respect, we must reckon that the hind-wings of *Ameletus* and *Oniscigaster* differ from their fore-wings, and also from both wings of *Protereisma*. The explanation probably lies in a shifting, at some fairly early point in the evolution of the hind-wing, of the point of attachment of the middle member of the triad, followed at a slightly later time by the development of a corresponding new tracheal supply.

#### ALTERNATIVE INTERPRETATIONS.

Having now considered all the evidence available under the three headings already indicated, we may ask whether any of them offer any basis for an alternative interpretation. The answer to this must be, that, in the case of the evidence from Convex and Concave Veins, and from the Fossil Record, there can be no doubt whatever as to the true homologies of the veins, and no alternatives to the solution here given can be offered. In the case of the larval tracheation, we have noted a considerable amount of variation both in the branch tracheal supply and in the mode of origin of the main tracheæ from the alar trunk. To anyone, therefore, who pins his faith upon this kind of evidence alone, and who refuses to admit that offered under the two other headings, alternative solutions are possible. The two chief alternatives, of course, are those given in the table on p. 145 as the Comstock-Needham and Morgan notations respectively. We may ask whether the evidence from the tracheæ alone does really support either of these two schemes rather than the one we have given in this paper.

With regard to the original interpretation given by Comstock and Needham, this clearly assumed that there had been a basal fusion between  $R_s$ ,  $M$ , and  $Cu$ . The evidence of the tracheation certainly supports the idea of a basal fusion between  $R_s$  and  $M$ ; but it shows clearly enough that  $Cu$  remains quite distinct. It does not seem necessary to say more about this alternative

notation, for the simple reason that its authors themselves admitted that it was unsatisfactory ; and, later on, they accepted Miss Morgan's interpretation instead (see Comstock, 1918, chap. x.). We have, then, only to consider Miss Morgan's notation. With respect to this, we may note the following points:---

(1) The research was carried out on wings of the last larval instar only. In this instar the tracheation is the most variable of all, and the posterior continuation of the alar trunk is usually absent. In spite of this, Miss Morgan correctly interpreted the homologies of the cubital tracheæ, but failed, for some reason, to connect them with their true venational homologues in the imago. Had she examined the tracheation in this region in earlier instars, she could not have failed to note the close correspondence between the strongly bent cubitus in the larva and imago ; and her results, as far as the limits of Cu were concerned, would then have agreed with those given in this paper.

(2) The evidence for her chief innovation, viz. the crossing of a simple Rs over two branches of M, as in Anisopterous Dragonflies, is not forthcoming from the great majority of the larval wings examined, but only from the wings of a single species, in which, as she admits (*l. c.* p. 98), "half of the wing-pads showed the radial branching just described and half of them gave no sign of it." The species which gave, in only one-half of its representatives, an indication of Rs crossing over M, was a species of *Heptagenia*, a genus which is by no means the most archaic of the fifteen genera studied by Miss Morgan. Yet she accepts this evidence, against the weight of evidence supplied by all the other fifteen genera and the other species of *Heptagenia* included !

As I have already pointed out, new light on the venation of Dragonflies has made it certain that Rs does not cross over M in the Zygoptera, and has also rendered it extremely improbable that the trachea which does this in the Anisoptera is Rs at all. The evidence for a crossing of Rs over M in Mayflies to be found within the Order itself is, as we have seen, practically negligible. Thus Miss Morgan's whole case totters to the ground, and must be replaced by a more lasting structure.

To sum up, we have seen how the evidence from the Convexity and Concavity of Veins agrees absolutely with that offered by a study of the Permian fossil *Protereisma*, and the combined evidence of these two lines of study is supported to a very great extent by that of the tracheation of larval wings, the only doubtful point in this latter evidence being its undoubted tendency to vary. Taken all together, the new system of homologies appears to me to be supported by so great a weight of evidence as to be at once acceptable in place of the hypotheses previously offered in the Comstock-Needham and Morgan notations respectively. At the same time it offers a new and clear basis on which to build up a system of classification within the

Order, which will present, to some extent at any rate, the real lines of evolution of the Mayflies through the long period of time from the Lower Permian to the present day. That problem may well be left to a later paper. I also hope to continue the series already begun on the venation of Odonata, and to show how, in that Order, the behaviour of the radial sector has followed the lines set out in this paper for the Mayflies, though very high specialisations of the Odonate venation have masked the original close similarity between it and that of Mayflies.

Cawthron Institute, Nelson,  
31 March, 1922.

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### *Venational Notation used in the Text-figures.*

1 A, first analis; 1 A<sub>1</sub>, 1 A<sub>2</sub>, its two branches. 2 A, second analis. 3 A, third analis. C, costal vein or trachea, separate from the costal margin. Cu, cubitus. Cu<sub>1</sub>, first cubitus; Cu<sub>1a</sub>, Cu<sub>1b</sub>, Cu<sub>1c</sub>, its principal triad in *Protereisma*. Cu<sub>2</sub>, second cubitus or vena dividens. cu-a, cubito-anal trunk trachea. cuf, primary cubital fork. hm, humeral brace, formed from the descending posterior branch of the costal vein. k, stump of Rs. M, media; M<sub>1</sub>, M<sub>2</sub>, M<sub>3+4</sub>, the three branches of its triad. M<sub>5</sub>, its posterior branch, forming the upper arm of the cubito-median Y-vein, the lower arm being Cu<sub>1</sub>. M<sub>5</sub> + Cu<sub>1</sub>, in *Protereisma*, the main stem of the cubito-median Y-vein, commonly called Cu<sub>1</sub>. mf, the primary median fork. Pc, precostal margin. R, radius; R<sub>1</sub>, its main stem or anterior branch. Rs, radial sector; R<sub>2+3</sub>, R<sub>4+5</sub>, its two main branches; further branchings are indicated, first by the four veins R<sub>2</sub>, R<sub>3</sub>, R<sub>4</sub>, R<sub>5</sub>, then by the suffixes *a* (anterior) or *b* (posterior) attached to any of these four veins, and finally by numerical prefixes 1 to 5, to avoid further suffixes. Sc, subcosta. sc-r, subcosto-radial trunk trachea. tn, tornus.

The Structure of Certain Palæozoic Dipnoi. By D. M. S. WATSON, F.R.S.,  
and E. L. GILL, M.Sc. (Communicated by Prof. E. S. GOODRICH,  
F.R.S., Sec.L.S.)

(With 34 Text-figures.)

[Read 30th November, 1922.]

THIS work began by an attempt to write an account of the structure of the Coal-Measure fish *Sagenodus* and *Ctenodus* on the basis of the splendid material in Newcastle. This collection when worked over by us left certain problems unsolved which have in part been cleared up by fossils in Edinburgh and elsewhere. During our search for this information we saw the splendid specimens of *Uronemus* in Edinburgh, and the wish for further light on certain morphological problems led us to extend the investigation to several other palæozoic Dipnoi.

The resulting paper now gives an account of the structure of these fish, which certainly includes the chief variants known to have occurred in the group, although some forms which might prove of great interest are still known to us only by the original descriptions or by unsatisfactory specimens.

With the possible exception of *Dipterus*, the most completely known of the fossil Dipnoi is now *Sagenodus*, and we therefore deal with that fish first, following on with an account of the related genus *Ctenodus*. For these two genera, the chief source of our material has been the Atthey Collection in the Hancock Museum at Newcastle-on-Tyne, but additional information of great importance has been derived from fine specimens in the Royal Scottish Museum and British Museum (Natural History).

The material is from the following horizons and localities:—

Lower Carboniferous (Oil Shale group): Broxburn, Loanhead, and other localities near Edinburgh—(*Sagenodus* and *Ctenodus*).

Upper Carboniferous (Westphalian): Newsham, Northumberland; Loughton, Staffs.; Ardwick, Lancs.; Newarthill, Lanarkshire; Linton, Ohio; Kansas—(*Sagenodus* and *Ctenodus*).

Upper Carboniferous (Stephanian): Nyran, Bohemia—(*Sagenodus*).

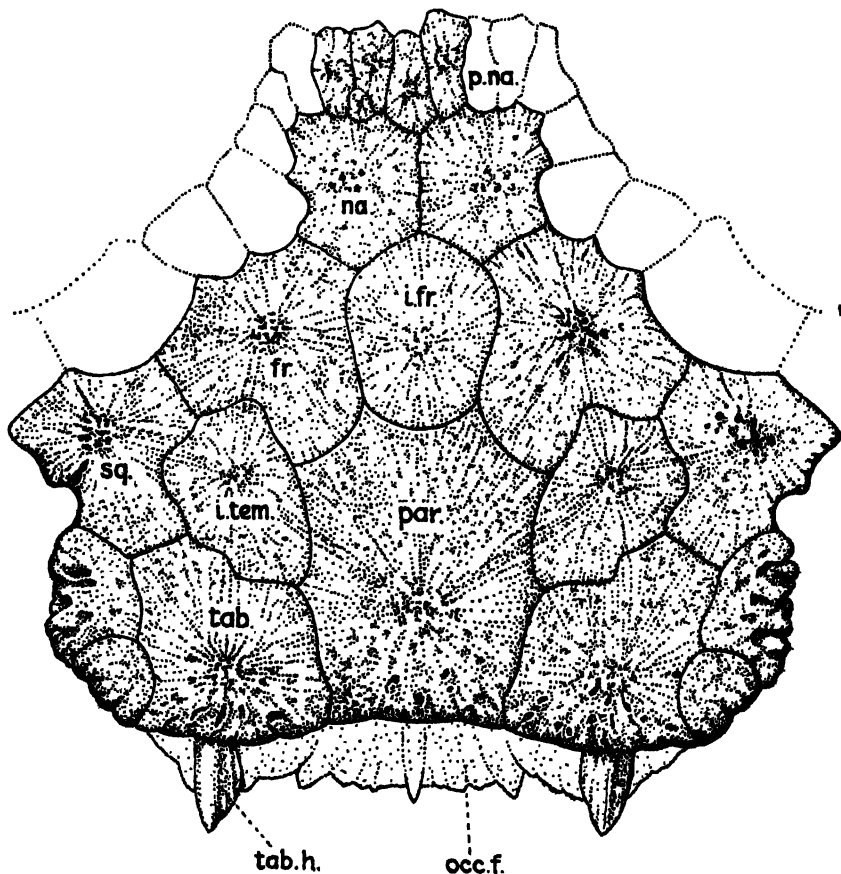
Lower Permian (Artinskian): Wichita, Texas; Kounova, Bohemia—(*Sagenodus*).

#### SAGENODUS, Owen.

Until the publication of Dr. Smith Woodward's second volume of the "Catalogue of Fossil Fishes" in 1891, the generic distinctness of *Sagenodus* from *Ctenodus* was not generally recognized. Nearly all the published work of any importance on the structure of these fishes appeared before that date,

and consequently in that work *Sagenodus* was usually referred to under the name of *Ctenodus obliquus*. The specific names *imbricatus*, *ellipticus*, *elegans*, and others, many of them probably synonyms of *obliquus* and of Owen's species *S. inaequalis*, were also applied by the earlier investigators to remains of *Sagenodus*; and more recently a large number of names of very doubtful value have been put forward, founded as a rule on isolated examples of the abundant and very variable tooth-plates.

FIG. 1.



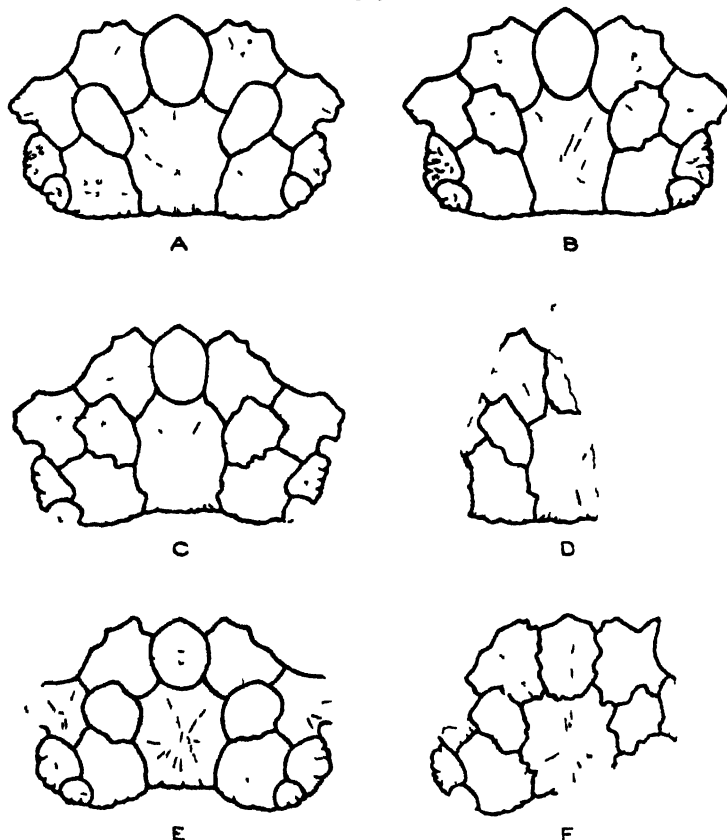
*Sagenodus*. Dorsal aspect of cranial roof,  $\times 3$ . Mainly from a specimen from the Low Main Seam of Newsham, in the Royal Scottish Museum. *fr.*, "frontal" (=frontal + post-frontal?); *i.fr.*, interfrontal; *i.tem.*, intertemporal; *na.*, nasal; *occ.f.*, occipital flange; *p.na.*, prenasal ossicles; *par.*, "parietal" (=parietal + dermo-supraoccipital); *sq.*, "squamosal"; *tab.*, "tabular" (=tabular + supratemporal); *tab.h.*, tabular horn.

What has hitherto been known of the structure of *Sagenodus* was due mainly to the investigations of Thos. Atthey and Albany Hancock (1863-1875). Important additions were made by L. C. Miall (1881). Fritsch, in

his 'Fauna der Gaskohle' (vol. ii. 1889), published numerous excellent figures of detached bones of *Sagenodus*, but a large proportion of them were unidentified, and his letterpress added little to what was already known. More recent contributions will be mentioned incidentally and in the List of Literature.

The available material has been re-examined by us, and the results are here stated, largely in the form of figures.

FIG. 2.



*Sagenodus*. Cranial roof of six individuals, to illustrate the extent of variation. A-D, Atthey Coll.,\* from the Low Main Seam, Newlam; E, F, Royal Scottish Museum, from the Virtuewell Seam, Newarthill.

In its general structure the skull of *Sagenodus* resembles that of *Ceratodus* in having an extensive cartilaginous neural cranium, of which no traces are ever to be seen, surrounded and supported by well-developed membrane supported bones. The bones which covered the top of the head frequently remain connected together in the fossils, but no complete articulated skulls are known.

\* Except where otherwise stated, the originals of all figures are in the Atthey Collection.

*The Roof of the Skull.*

It has been customary to dismiss the cranial roof of *Sagenodus* and *Ctenodus* as being composed of numerous small bones of rather indeterminate arrangement and doubtful homology, though bearing a considerable resemblance to those of the roof of the skull in *Dipterus*. Incomplete skull-roofs of both genera were described, but not figured, by Hancock and Atthey (1872, p. 401), who clearly stated some of the points distinguishing skulls of *Ctenodus tuberculatus* (i. e. the genus *Ctenodus* as now understood) from those of *C. obliquus* (i. e. *Sagenodus*). Rough figures of the posterior roof-bones of the *Sagenodus* skull were given by T. P. Barkas (1873, figs. 244-246) and Miall (1881, fig. 1). Miall's figure was good as far as it went, except in the region of the bones that we call the intertemporals, where it is probable that he was misled by false suggestions of sutures. In a large number of examples, at any rate, we have met with no similar case, though monstrosities do occasionally occur (cf. fig. 6, A and C, p. 170).\*

Of Barkas's three figures, 245 evidently represents the same specimen as was used by Miall for the right side of his figure, while fig. 246 represents a fragment seen from the underside and showing the shape regularly assumed underneath by the suture at the front of the "parietal." His fig. 244, that of the hinder two-thirds of a skull-roof, is correct on the whole, but the posterior corners are missing; the original is now in the British Museum (No. 45852).

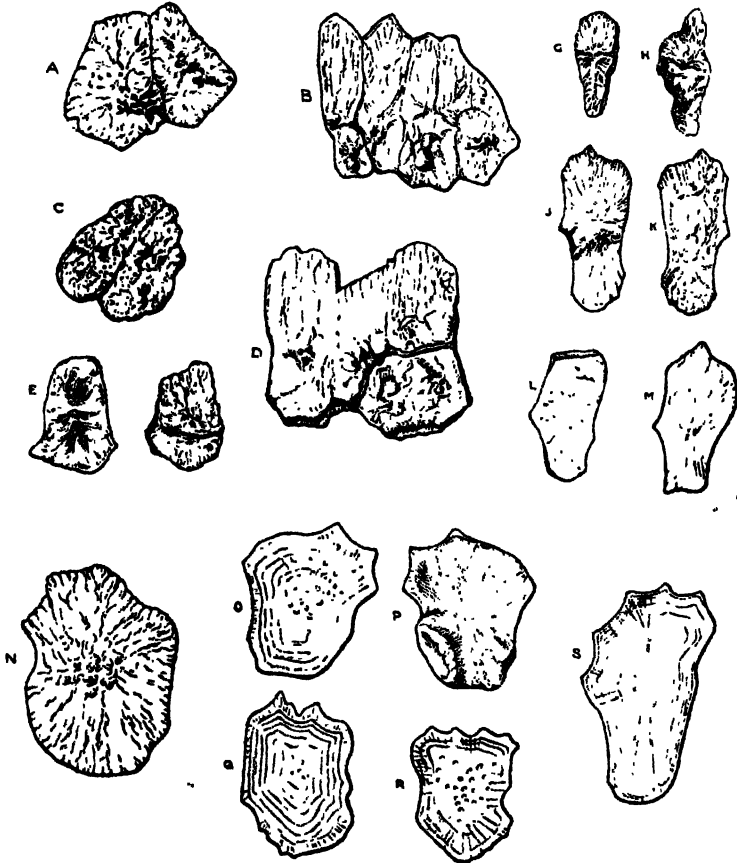
The length of an average skull-roof is about  $5\frac{1}{2}$  inches (14 cm.), but some were rather larger. The figure here given (fig. 1, p. 164), together with the variations represented in fig. 2, renders unnecessary a detailed description of the form of the bones. The bones are named in accordance with the suggestions of Watson and Day (1916, p. 42). Their degree of variability may be estimated by comparing the outline of any one bone through the series of figures, each drawn from an actual specimen, given in fig. 2, p. 165. It will be seen that though there is wide variation in details of shape, there is never any difficulty (apart from rare monstrosities) in recognizing single bones detached from the skull.

In the state in which they occur in the shales the bones of the skull-roof are about 4 mm. thick in full-sized heads. Neighbouring bones are locked together by means of thin laminae, radially ribbed, springing from almost the lowest level of the thickness of the bones and fitting into the adjacent bone at the same level. Mr. H. Fletcher, late of the Zoological Museum, University College, Reading, tells us that the bones in the skull-roof of *Ceratodus forsteri* are articulated in the same way. On the inner surface of the roof some bones encroach upon others further than they do outside, so that though the pattern on the two surfaces is nearly the same it is never identical.

\* In fig. 6, A, the right frontal (*fr.r.*) is quite abnormal in shape, and in fig. 6, C, the left intertemporal has entirely vanished, the region in which it should be being occupied by an enlargement of the bones which normally surround it.

The inner face of the roof-bones has a polished surface and usually bears radiating ridges. The outer face varies a good deal in surface character, but it is generally granulated, with a varying degree of gloss, and shows fine lines radiating on each bone from a central pit or rosette. Bundles of these lines often run from the rosette of one bone to that of the next. Rosettes are always more strongly developed on the frontal and squamosal than on the other bones. The whole appearance of the bones suggests that the head was

FIG. 3.



*Sagenodus*. Nasal and prenasal bones. Q and R after Fritsch, all the rest from specimens in the Atthey Collection from Newsham,  $\times$  about  $\frac{1}{2}$ .

A-M, prenasal-ossicles: F, G, H, J, under surface, the rest dorsal aspect.

N-S, nasals: P, under surface of O; S, a remarkable form which would not fit into any skull yet seen.

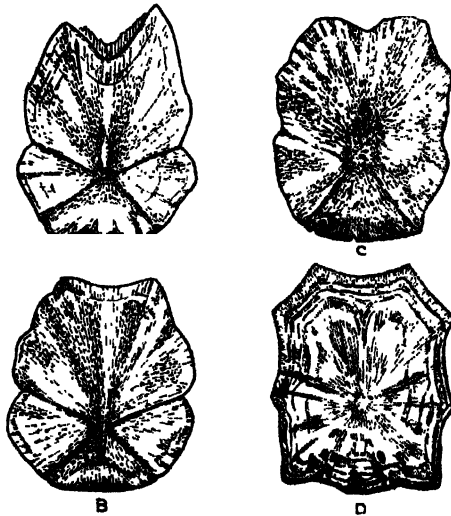
covered only by a thin skin, and not, as in *Ceratodus*, by scales. This supposition is confirmed by the occasional appearance of the grooves of sensory canals on the skull-roof. A well-marked lateral-line groove is seen to run from the rosette of the "parietal," first to the rosette of the



intertemporal and then to that of the squamosal. This groove is for a line of pit organs, found also in *Ceratodus*. Such grooves are independent of the bundles of striæ already referred to. The corresponding bones of very young individuals show these grooves much more plainly (see fig 4, A, B, C, below). The course of the grooves, when they appear at all, is precisely that of the sensory grooves marked on the skull of *Dipterus*.

One common type of skull-roof is not represented in fig. 2, p. 165, because it apparently always came to pieces in fossilization, and is hence only known by detached bones. It is characterized by the high polish of the external (as well as of the internal) surface of the bones, by their simplified outline, and by the conspicuous zonal bands near their margins. A fish of this type was evidently the predominant *Sagenodus* in Fritsch's collection from the

FIG. 4.



*Sagenodus*. Parietals,  $\times$  about 3. A and B, of very young individuals, show well-marked lateral-line grooves and illustrate the scale-like form of the young bones; C is of a rather older individual; D is a bone of the zonal and polished type; though small, it has the adult form.

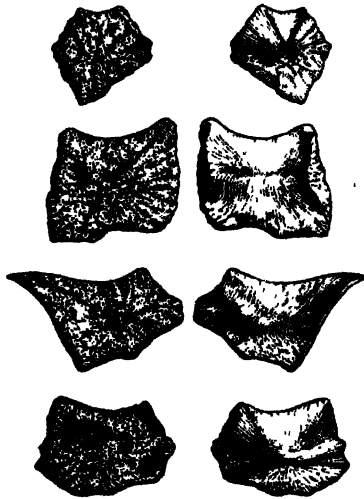
Gaskohle; in the Atthey Collection it is comparatively scarce and usually of very small size, but a few large "parietals" prove that in the Northumbrian coalfield, as in the Bohemian, it reached the same size as the other forms. A very small "parietal" of this zoned and polished type is represented in fig. 4, D, above.

The posterior margin of the skull-roof presents as a rule a concave outline, sometimes pronouncedly so (fig. 2, E & F, p. 165; fig. 18, A, p. 183). In a few cases it is nearly straight or even slightly convex. A pair of tabular horns for the attachment of the shoulder-girdle are conspicuous at the back of a well-preserved skull. At the level of the inner face of these horns there is a thin frill of bone (fig. 1, p. 164, *occ.f.*) stretching across the

whole hinder border of the skull. It springs from the three hindermost roof-bones, not at their actual edge, but from a little way forward on the under surface, and along this line the extreme hind border of the bones is frequently cracked and bent down in fossilization. It is possible that in life this thin flange stood vertically, more or less at right angles to the skull-roof, and overlapped the hinder surface of the neural cranium.

From the outer hind corner of the tabular forward to the outermost point of the squamosal the edge of the skull-roof is rounded off and usually lobed and corrugated, except for a smooth and very definite notch in the border of the squamosal. It is along this part of the roof that the operculum is hinged

FIG. 5.



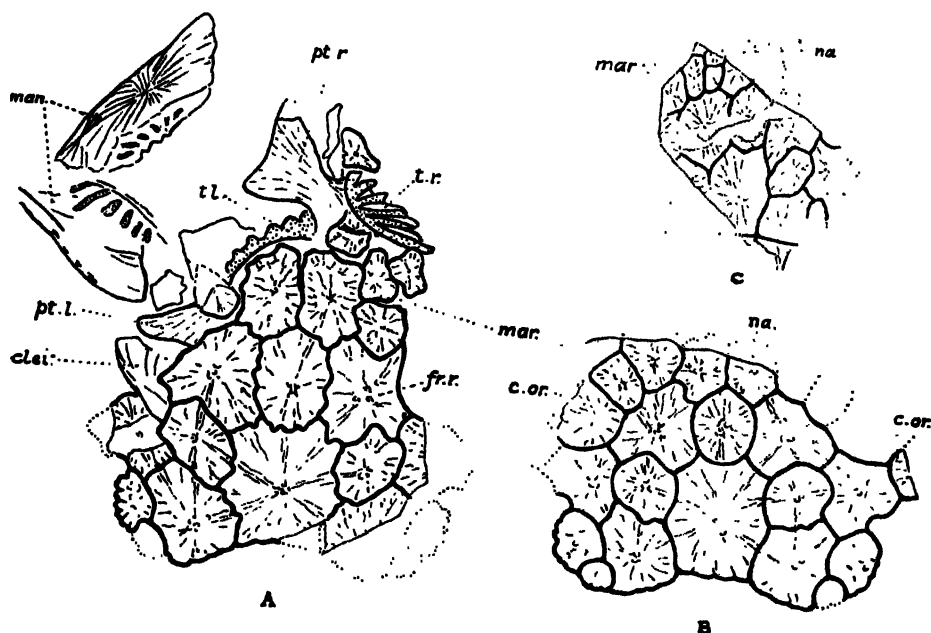
*Sagenodus*. Circumorbitals,  $\times$  about  $\frac{1}{3}$ .  
Outer faces on the left, inner on the right.

(see fig. 18, p. 183). The notch in the squamosal lodges the anterior knob of the operculum, and the two bones forming the hinge-line behind the notch bear on their under surface a groove, bounded internally by a ridge, which engages a flange borne by the operculum along its upper border. The posterior knob of the operculum, more or less strongly developed, fits against the hinder end of the smaller corrugated bone close to the corner of the tabular.

From the outer point of the squamosal forwards the edge of the skull-roof everywhere shows articular faces, with articular laminæ where the bones are well preserved. It is here that the orbitals and other marginal bones were attached. As a rule, however, the marginal bones, and the nasals as well, have been lost, even where the main part of the skull-roof has held together. Probably this main part (represented in the outlines in fig. 2, p. 165), was flat or nearly so, whereas the bones bordering it would be

articulated with it on a downward curve, and would be subjected to much greater strains during the maceration undergone by the skull before its burial. The nasals are shown in their natural position in several skulls in the Royal Scottish Museum; one skull from Newsham, in the same museum (No. 1878.45.7), shows several prenasal ossicles in position as well. They are introduced in fig. 1, p. 164. In the Atthey Collection there are a number of detached nasals and prenasals. Both are much more variable in shape than the other bones of the skull-roof behind them (see fig. 3, p. 167). All the prenasal ossicles seem to be crossed on the underside by a ridge and groove (fig. 3, F, G, H, J, p. 167), which may mark the position of a lateral-line canal.

FIG. 6.



*Sagenodus*. Outlines of specimens, showing marginal ossicles and circumorbitals.

A. From the Virtuewell Seam, Newarthill, Lanarkshire. Royal Scot. Mus. (1897/110/31).

*pt.r.* & *pt.l.*, right and left pterygoids with their teeth *t.r.* & *t.l.*; *man.*, mandible.

B. From the same horizon and locality as fig. A. R.S.M. (1897/112/5).

C. Coal Measures, Linton, Ohio, U.S.A. British Museum (N.H.) (P. 7773).

### *Circumorbitals and Marginal Ossicles.*

These bones frequently occur scattered among the other bones in disarticulated examples of *Sagenodus* on slabs of shale, and in the Atthey Collection there are large numbers of them in this sort of association or as isolated bones freed from the matrix. Many of them were certainly orbitals, for they have one of their edges thinned out and rounded, and leading on the

underside to a hollowed and polished surface. Four of the commonest patterns (of each of which there are several duplicates) are represented in fig. 5, p. 169. It will be noticed that the radius of curvature of the orbital notches is far from uniform, apart from questions of size of bones, which seems to indicate that the orbit cannot have been circular. One skull in the Atthey Collection (fig. 18, A, p. 183), several in the Royal Scottish Museum (*e.g.* fig. 6, A, B, p. 170), and one fragment from Ohio in the British Museum (fig. 6, C, p. 170), show some of the orbital and other marginal bones in top view in articulation with the skull-roof, but no specimen we have yet seen gives much help in reconstructing the orbit itself. The hypothetical arrangement which we suggest in fig. 20, p. 186, is chiefly based on an examination of the bones themselves, taking account of the edges bearing orbital notches, the edges with articular faces, and the edges which were evidently free. It accounts for all the recognizable types of circumorbitals which occur in the Atthey Collection. Some of the skulls referred to above show that the smaller marginal bones articulating with the nasals and with the fore-part of the frontals did not enter into the orbit, and we have accordingly represented them as intermediate roofing ossicles.

#### *The Palate.*

Neither we nor previous workers have found indications of any kind of ossification of the brain-case, which must have been as completely cartilaginous as it is in *Ceratodus*. Where the skull-roof and the palate are undisturbed they lie directly one upon the other, usually with hardly a trace even of the matrix between them.

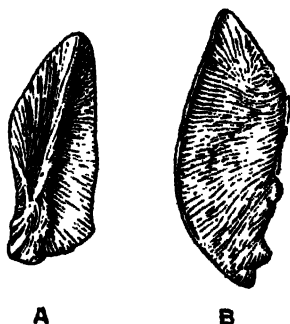
The bones of the palate have been well known for many years, and the additional observations that we have to make refer mainly to certain details of their relations to one another. Like all the other bones of *Sagenodus*, the parasphenoid is very variable in form within definite limits, and especially so in regard to the development of a median ridge on the buccal face of its main "lozenge" and in the shape and prominence of the lozenge at its hinder angle. Common types are represented in fig. 9, p. 174. The parasphenoids collected at Newsham were supposed by Hancock and Atthey to belong to about half-a-dozen distinct species, a view which Miall dissented from, though it is not without some measure of support.

Even before the existing *Ceratodus* became known, it was seen in a general way how the pterygoids with their tooth-plates must have fitted round the lozenge of the parasphenoid. Attempts to depict the bones in their natural position have not, however, been altogether happy. Miall's restoration (1874, pl. 47), which is based on the similar palate of *Ctenodus*, is the most successful, but he shows the hinder ends of the pterygoids projecting as loose frills beyond the lozenge. Williston's figure (1899, pl. 37, fig. 2) has the same defect, and in addition his pterygoids lack most of their hinder wing.

and he shows the parasphenoid with its cranial face turned to the mouth. The cranial and buccal faces of the parasphenoid had been correctly identified by Miall (1881, fig. 3).

The way in which the pterygoids actually fitted on to the parasphenoid is perfectly shown by two specimens in the Royal Scottish Museum (Nos. 1902.73 and 1894.168.2). These actually belong to an early form of *Ctenodus* (the form to which Traquair applied Barkas's name *Ctenodus interruptus*); but as this form had the palate of a *Sagenodus*, and as the differences between typical palates of the two genera are in any case slight, it is appropriate to refer to them here. The more perfect of the two specimens is depicted, from a rough sketch, in fig. 24, p. 193. It shows that the lateral corners of the parasphenoid lozenge, looked at from the buccal aspect, overlay the edges of the pterygoid, but that towards the front of the lozenge these edges passed on to its buccal face and met each other across it by a square corner at the hinder end of their symphysis. Well-preserved examples of the

FIG. 7.



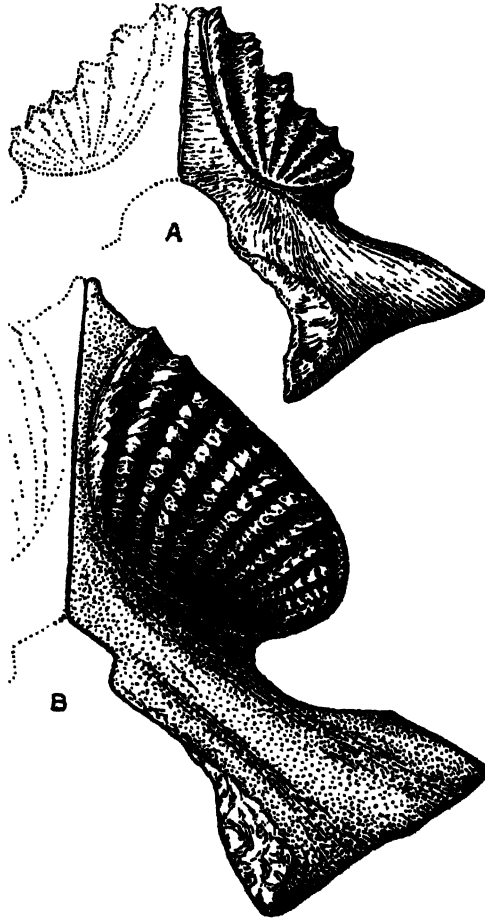
*Sagenodus*. Sub-operculum,  $\times \frac{1}{2}$ . A, outer surface; B, inner surface of another example.

pterygoid (fig. 8, A, p. 173), as a matter of fact, always show a roughened surface corresponding to the corner of the parasphenoid to which they were articulated. (It is of the same character as the corresponding narrower surface on the pterygoids of *Ceratodus*, and has been figured by Atthey and by Williston.) They also show the corner at the hinder end of the symphysis by which they met their fellow across the face of the parasphenoid, and the imprint of these corners is occasionally visible on a detached parasphenoid. It is only in "*Ctenodus interruptus*" that the corner is square. In other forms both of *Ctenodus* and *Sagenodus* it is obtuse and meets its fellow in a forwardly-pointing angle. The arrangement of the elements of the palate in a typical *Sagenodus* is seen in fig. 10, p. 176.

The meeting of the pterygoids across the front of the parasphenoid may in part explain the singularly weak pterygoid symphysis. In *Ceratodus* the pterygoid symphysis is very much stronger than that of the lower jaw; in *Sagenodus* it is altogether weaker, for the bones meet only in a long, thin

edge. At the back, however, this weak symphysis is supported on the cranial face for some part of its length by the anterior process of the parasphenoid, though that still leaves the forward part and the long anterior ridges of the tooth-plates to all appearance very insufficiently provided against the strains of mastication. This region, however, no doubt received further support from the overlying cartilaginous cranium.

FIG. 8.



A, *Sagenodus*; B, *Ctenodus*. Left pterygoid and tooth-plate,  $\times 3$ .

As they occur in the shales, the pterygoids and their tooth-plates are nearly always crushed into one plane. There can be no doubt, however, that in life the wing of the pterygoid would be bent downward along its outer edge to support the quadrate. It may not have been bent so sharply as in *Ceratodus*, where it stands at right-angles to the tooth-plate, but that it was considerably bent is proved by the abundant cracks that break the

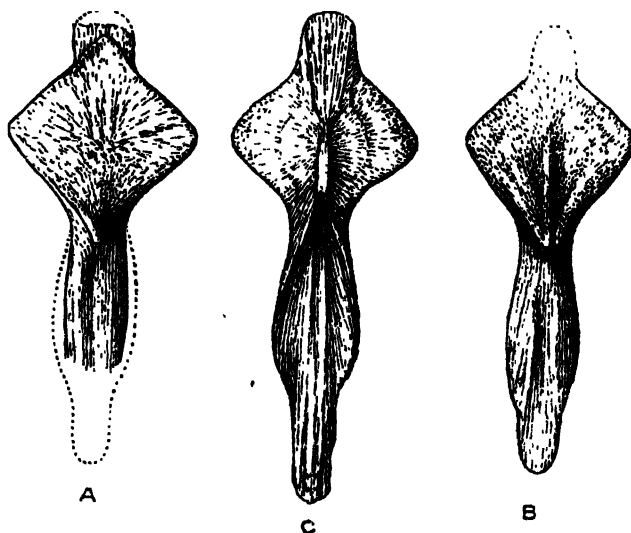
surface of these flattened bones, as well as by the curve actually shown by the least crushed examples—among them some very small pterygoids which by their minuteness have escaped the worst of the crushing.

The facet on the "toe" of the pterygoid was remarked upon by Miall (1881, p. 292). It is precisely like the corresponding facet in *Ceratodus*, except that in *Ceratodus* the facet itself is composed of cartilage; and it doubtless had the same function, namely to support the quadrate and strengthen the articulation of the lower jaw.

### *The Quadrate.*

The bone which we take to be the quadrate has long been known as a bone of *Sagenodus*, but has been assigned to various positions. Fritsch

FIG. 9.



*Sagenodus*. Parasphenoids,  $\times$  about  $\frac{1}{2}$ .

A and B, palatal surface (B, the commoner type); C, dorsal surface.

usually identified it as a scapula ("Schulterblatt"), as in his Taf. 77, figs. 1 and 4 (1889), but another example, Taf. 77, fig. 12, is labelled "Femur?". The same bone was well figured by Williston (1899, pl. 28, fig. 3), who suggested that it might be the ceratohyal. It is a large bone in proportion to the size of the head, but in a Dipnoan with a head deep enough to accommodate such an operculum as that of *Sagenodus* the quadrate would necessarily be large. Even as it is, there is evidence that its upper end was incompletely ossified. The ossification of the rest of the bone, too, was more or less superficial, though carried much further than in the quadrate of *Ceratodus*. As they are found in the shales, the bones have always collapsed under pressure as the core of cartilage decayed.

Fig. 11, C and D, p. 177, show good examples from the Low Main shale, Newsham, in the Atthey Collection. Both ends of the bone were expanded, the lower more so than the upper. One side of the shaft bore a pronounced longitudinal ridge or wing, better preserved in Williston's and some of Fritsch's examples than in ours. The aspect shown in fig. 11, C, p. 177, we take to be the inside of a right quadrate, and we suggest that the facet on the toe of the pterygoid was applied to the prominence there shown at the lower end of the bone on the right, possibly also engaging with part of the longitudinal wing.

We have been unable to identify any further bones as belonging to the skull proper. *Vomerine teeth* were described and figured by Atthey (1877), and we see no reason to doubt his identification; but no trace of bone is attached to these teeth, and it is probable that the vomers were represented solely by the bases of the teeth, as in *Ceratodus*.

We have not been able, either, to identify any of the hyoid bones with certainty. Many large rib-like bones occur on slabs of shale among the other remains of *Sagenodus*, and there can be little doubt that some of them are hyoids, others probably cranial ribs. Fritsch was confident that he had identified both; the bone he named "first cranial rib" (1889, Taf. 77, fig. 5) may well be such, but some of his "hyoids," especially that figured at Taf. 71, fig. 5, are probably not bones of *Sagenodus* at all\*.

#### *The Lower Jaw.*

The main features of the structure of the lower jaw were made out many years ago. Hancock and Atthey described and figured the "splenial" in 1872; and in 1877 Atthey announced the discovery of the angular ("articular"), which he had been able to identify by comparison with the newly-discovered *Ceratodus forsteri*. To complete the resemblance of the jaw to that of *Ceratodus*, a "dentary"† element was needed, and its existence in *Sagenodus* was first demonstrated by Watson and Day (1916), who found it in the form of a broken cross-section fitting on to the front of the angulars in a head in the Manchester Museum (L. 10904). In the Atthey Collection we have found an abundance of examples of the bone itself, some lying among the other remains of crushed heads and many others freed from the matrix. In the Dinning Collection, also in

\* Fritsch believed (p. 67) that he could recognize the bones of "*Ctenodus obliquus*" with certainty by their lustre and colour, and in a few instances this criterion possibly led him astray.

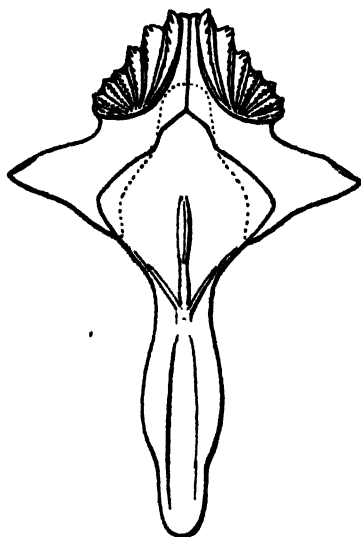
† As will appear from a later discussion of the jaw of *Dipterus*, there is good ground for thinking that the bones here referred to as "splenial" and "dentary" are not properly so named. But since, following Huxley (P. Z. S. 1876, p. 34), the corresponding bones in *Ceratodus* have long been known by those names, we retain them in this description, only placing them in quotation-marks.



the Hancock Museum, there is a small angular with the "dentary" still in natural articulation with it. This specimen bears a label in Atthey's handwriting, and as he called it simply "*Ctenodus*, articular bone," he presumably thought it merely a damaged or aberrant angular. It is represented in fig. 14, p. 180.

The figures here given will make it unnecessary to describe the jaw at length. Restorations in different aspects are given in fig. 12, A, B, C, D, p. 178, and corresponding views of the lower jaw of *Ceratodus*, after removal of the cartilage, are given in fig. 13, p. 179. It will be seen that apart from the difference in the tooth-plates the two jaws are remarkably alike. The bones in *Sagenodus* are very much stouter, but that is a difference that obtains in nearly all parts of the skeleton.

FIG. 10.



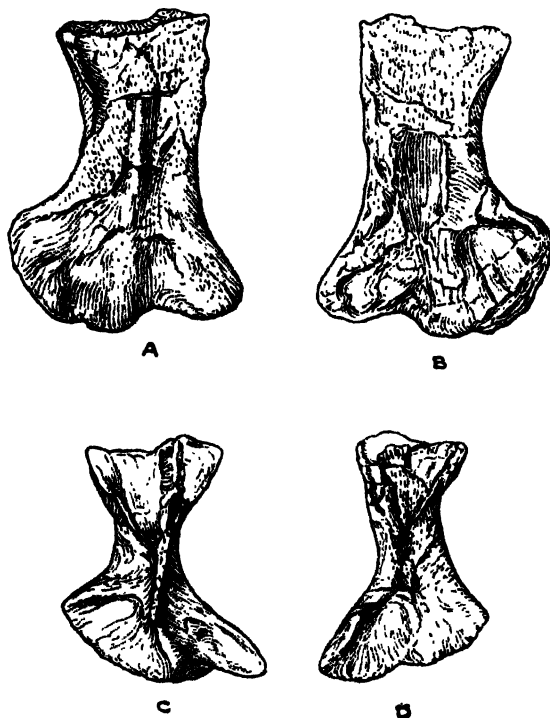
*Sagenodus*. Reconstruction of palate, showing pterygoids in natural articulation with the parasphenoid. The postero-lateral wings (quadrate rami) of the pterygoids are shown flattened into the same plane as the parasphenoid.

The bones that differ most in the two forms are the "dentaries," for though they are much alike as seen from below, the "dentaries" in *Sagenodus* take a more essential share in forming the jaw than they do in *Ceratodus*. In the latter fish they are papery bones feebly connected with the angulars by a very slight groove near the edge. In *Sagenodus* (fig. 15, p. 180) they are strong bones firmly united with the angulars, which have a pronounced groove for their reception along the anterior half of their lower edge. But the most striking difference in the "dentaries" of the two fishes

lies in the form of the hind border. In the "dentary" of *Ceratodus* this border is thin and papery like the rest of the bone. In the *Sagenodus* "dentary" it is widened abruptly, and presents a deep, polished face toward the gular space (fig. 15, D, p. 180). This part of the jaw is, in fact, finished off in almost precisely the same way as the corresponding part in *Dipterus*, and, as we show later, for the same purpose: to form a bearing for gular plates.

All the elements of the jaw are as variable as the teeth have long been known to be. Fig. 12 E, p. 178, shows that some jaws are deeper than that figured above it at C, and certain angulars in the Atthey Collection would fit

FIG. 11.

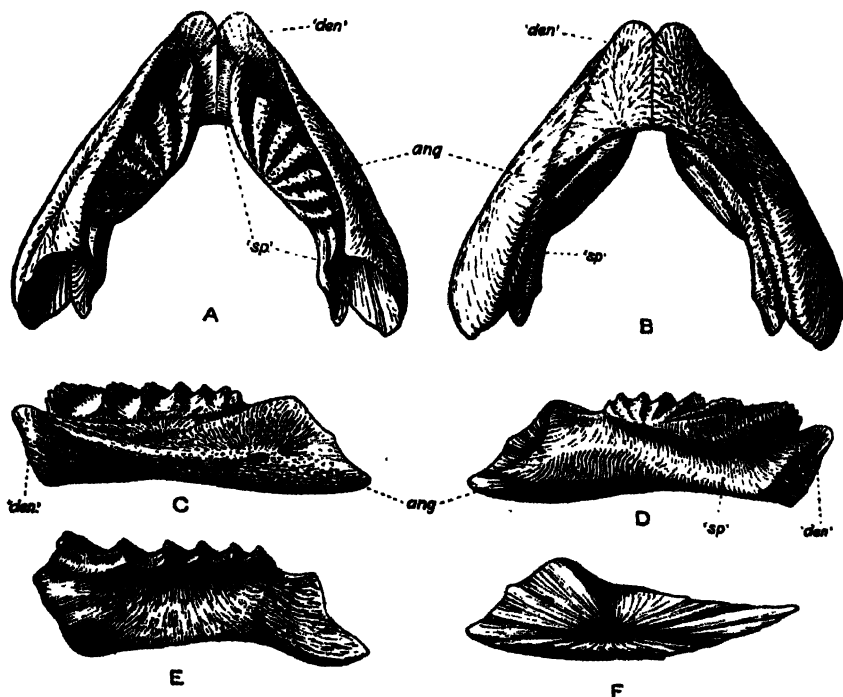
Supposed Quadrates,  $\times$  about  $\frac{1}{2}$ .

A, B. Supposed to be of *Ctenodus*. C, D. *Sagenodus*. (A and B are opposite sides of the same specimen: C and D are opposite sides of two different specimens.)

a jaw of this deeper form. Other angulars suggest an even shallower jaw than C. Well-preserved angulars show that both the upper and lower borders of the bone were rolled inwards very considerably; the lower part towards the middle of its length formed a sort of floor inside (fig. 12, F, p. 178), and the upper edge bears a bracket for the support of the back of the tooth-plate, as was noticed by Atthey (1877, p. 228). Very small angulars, of 3 or 4 cm. in length, not having been seriously crushed, exhibit this inward

rolling of the upper and lower borders very markedly. The "dentaries" are even more variable than the other bones of the jaw, both as regards shape and surface character. Three different patterns are shown in fig. 15, p. 180. The "dentary" there marked C is one of the shortest in relative length and deepest at the symphysis; some are even narrower than the one figured at A. The symphysis itself is commonly of the character shown in D, much like that of the "splenial" in fact; but a quite different type occurs in which the "dentaries" were united by interlocking spines, as shown at A. The

FIG. 12.

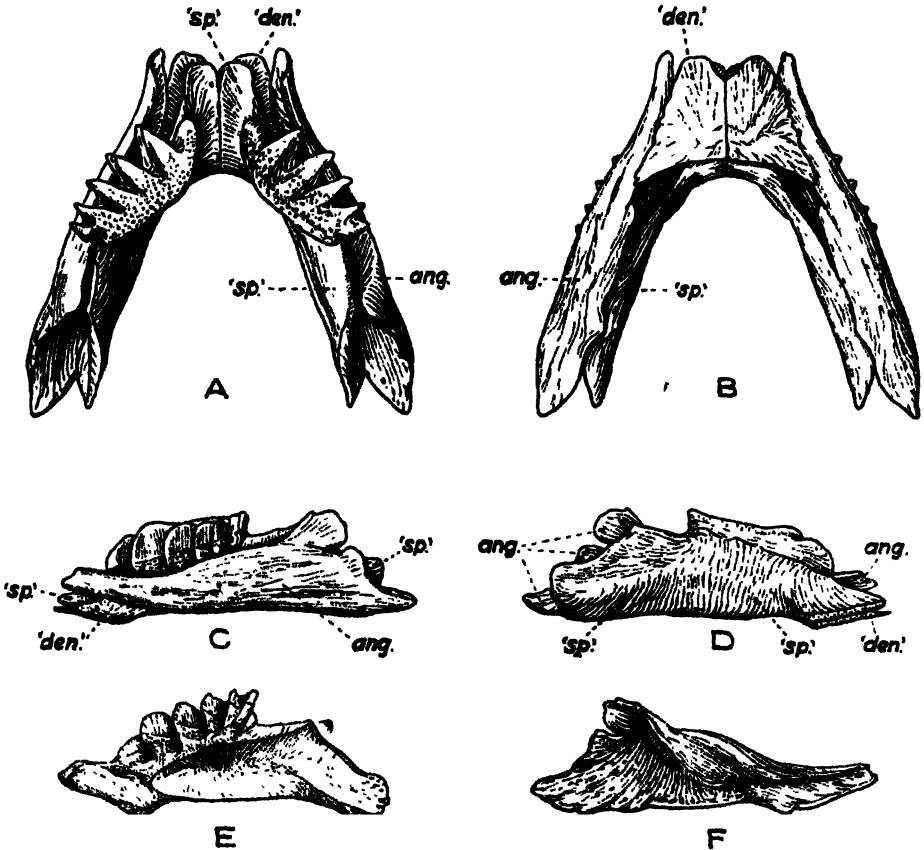


*Sagenodus*. Reconstruction of lower jaw,  $\times \frac{1}{2}$ . A, dorsal, B, ventral, C, lateral, D, medial aspects; E, "splenial," from the outer side; F, angular, from the medial side; *ang.*, angular; "*den.*," "dentary" (=splenial); *sp.*, splenial (=pre-articular). (Compare with figs. 13 of *Ceratodus* and 27 of *Ctenodus*.) E is *S. imbricatus*; the rest of the figures *S. obliquus*. The deep symphysis of E can be matched in the latter species.

line of sensory pits in the angular is often continued on the "dentary," and where this is the case one of the pits seems regularly to lie on the suture (fig. 14, p. 180). Near the posterior border of the "dentary" there is often a row of three or four much smaller pits. In some pairs of "dentaries" the posterior borders would apparently meet across the middle line in an even curve; in others these borders are strongly hooked at the

symphysis, sometimes considerably more so than in fig. 15, C, p. 180, and together they must have produced a small backward process at the middle line (fig. 16, B, p. 181), a difference that would be reflected in the shape of the gular plates which adjoined the "dentaries" behind.

FIG. 13.



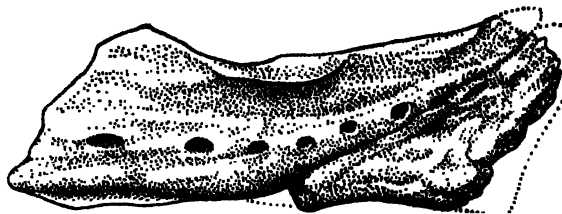
*Ceratodus (Neoceratodus) forsteri*. The bones and tooth-plates of the lower jaw. A, dorsal, B, ventral, C, lateral, D, mesial aspects; E, "splenial," from the outer side; F, angular, from the mesial side. (Reference letters as in fig. 12.)

### The Gular Plates.

The absence of gular plates has been given as one of the diagnostic points separating the Ctenodontidæ from the Dipteridæ. The similarity of the hinder border of the "dentaries" in *Sagenodus* and *Dipterus* led us, however, to look for something in *Sagenodus* to correspond with the gulars which are applied to this border in *Dipterus*, and this we believe we have found in the bone represented in fig. 16, A, p. 181. There are three examples of this bone in the Atthey Collection. One of them occurs on a slab of shale

among the scattered but practically complete remains of a head of *Sagenodus*; the other two are detached. It is a bone of graceful form, delicately striated on one face in lines converging towards a small tubercle near the blunt end. The other face is smooth. Fig. 16, B, p. 181, shows the size of the bone in relation to the lower jaw and the manner in which we suggest that it fitted

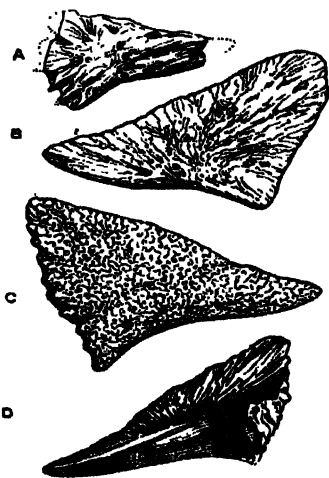
FIG. 14.



*Sagenodus* sp. Right angular and "dentary" in natural association,  $\times 1\frac{1}{2}$ .

in the gular space. Compared with the extensive gular apparatus of *Dipterus*, described later, it is meagre, but it is much what might be looked for in a fish which in so many respects is a transitional form between the early Dipnoi and *Ceratodus*.

FIG. 15.



*Sagenodus*. A, B, C, outer surface of three "dentaries,"  $\times$  about  $\frac{2}{3}$ ; D, inner surface of a left "dentary," oblique view showing the character of the symphysis and of the hinder border.

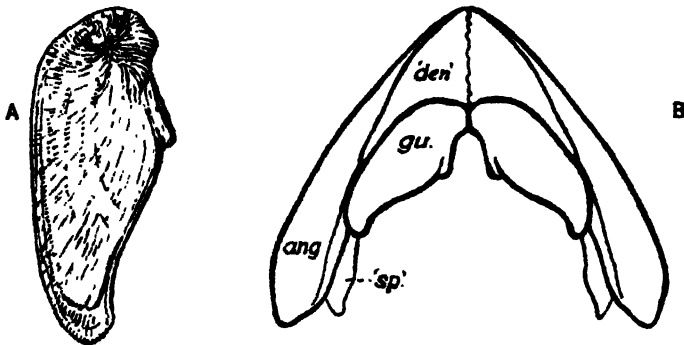
### *The Opercular Bones.*

Next to the teeth, the operculum is probably the best-known of the remains of *Sagenodus*. In proportion to the head as a whole, it is remarkable for its size and massiveness. Its manner of attachment to the skull has been described already (p. 169). In common with the other bones, it varies greatly

in outline, but the form shown in fig. 20, p. 186, is a good average. The variation consists for the most part in the greater or less development of the hinder lobe of the bone. There is every gradation, independently of size, from a form in which the body of the bone is fairly symmetrically disposed under the centre of the hinge-line, to an extreme but quite common pattern in which the hinder border is so prominent that the centre of the bone lies below the posterior knob, behind the hinge-line altogether. In this latter pattern of operculum the posterior knob is always greatly developed and the anterior one almost obsolete. Opercula of this type have been figured by Miall (1881, fig. 7, where they are shown upside down); and by Williston (1899, pls. 35 & 36) in his description of *S. copeanus*.

A small bone, hitherto undescribed, which we take to be the *Sub-operculum*, occurs in several of the crushed heads of *Sagenodus* which we

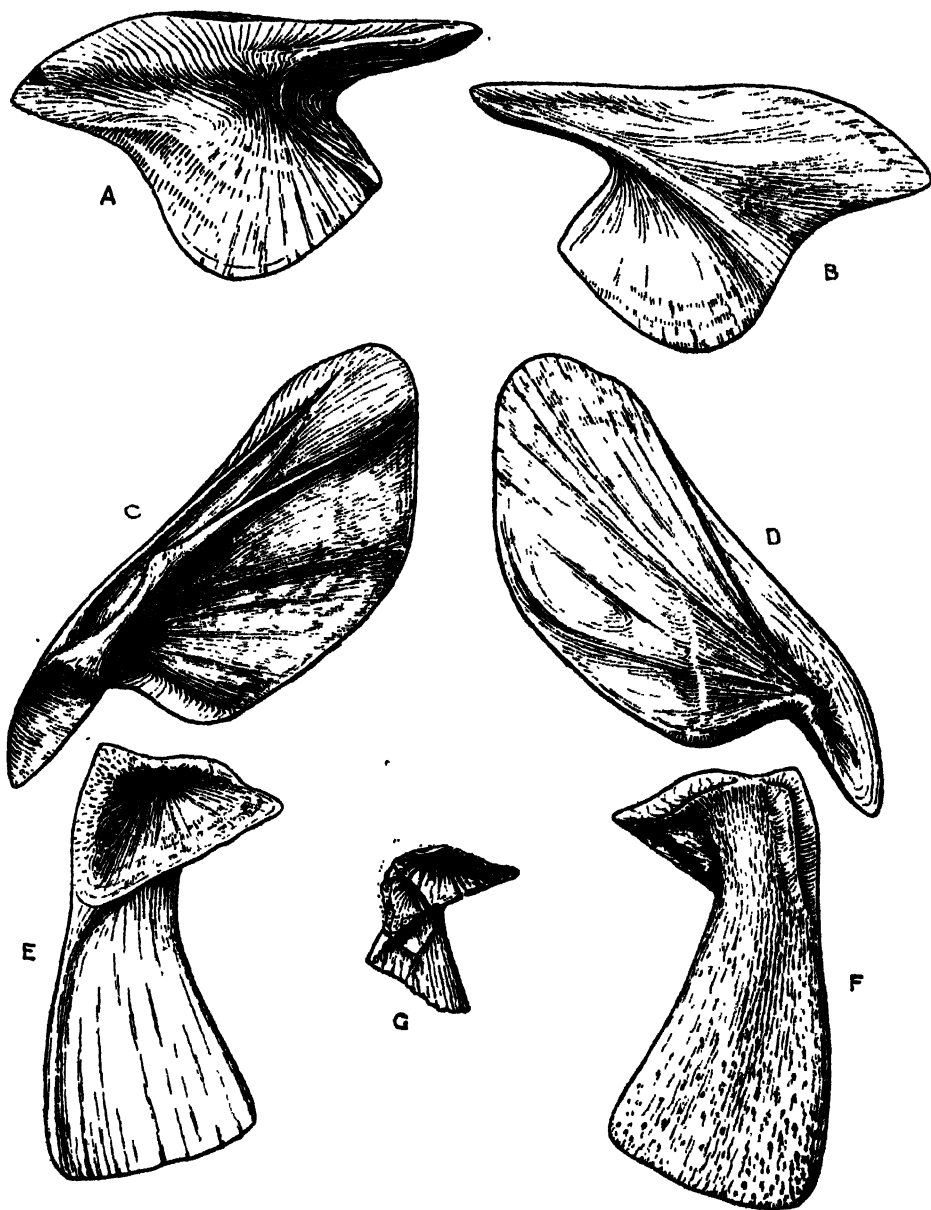
FIG. 16.



*Sagenodus*. A, left gular, inner surface: B, diagram, showing the probable position of the gulars.

have examined; it is shown, for example, on the slab, part of which is represented in fig. 18, p. 183, and in the head in the Manchester Museum (L. 10904) described and figured by Watson and Day (1916). It is a bone of an inch to an inch-and-a-half in length in an average skull, and is recognizable by its triangular point (see fig. 18, A, p. 183). Completely preserved examples, such as those represented in fig. 7, p. 172, show that half the bone was fairly thick and strengthened by a rounded ridge, while the other half consisted of a thin flange which might easily be lost. Its disappearance would give the rest of the bone a much more pointed shape, such as is seen in fig. 18, p. 183. The sub-operculum of *Ceratodus* (inter-operculum, Huxley), to judge by a dried skull, would much resemble this bone if its cartilaginous fringes were ossified. No specimen that we have seen shows this bone in its natural position, but on two out of the three slabs on which we have found it, it lies close to the squamosal, which may indicate that it was applied to the front rather than to the hind border of the

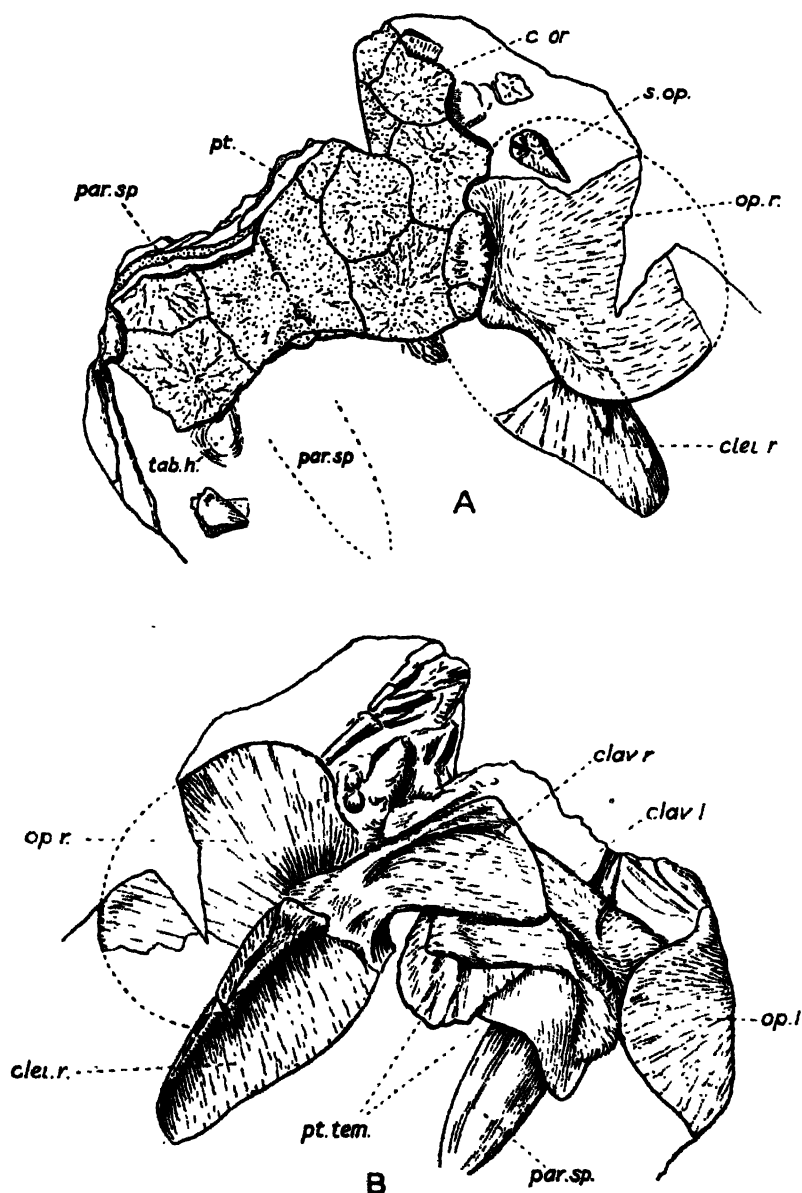
FIG. 17.



*Sagenodus*. Bones of the shoulder-girdle. A, right post-temporal, outer surface; B, the same, inner surface; C, right cleithrum, outer surface; D, the same, inner surface; E, right clavicle, upper (chiefly internal) surface; F, the same, lower surface; G, right clavicle, imperfect, to show the cracks which result from the flattening of the bone. In E and F the bones are represented as flattened, but without the cracks.  $\times \frac{1}{2}$ .

(The elements of the shoulder-girdle are seen in natural association in fig. 19, p. 185.)

FIG. 18.



*Sagenodus*. Anterior portion of a specimen in the Atthey Collection,  $\times$  about  $\frac{1}{2}$ . A, dorsal B, ventral surface. *clav.l.*, left clavicle; *clav.r.*, right clavicle; *clei.r.*, right cleithrum *c.or.*, circumorbital; *op.l.*, left operculum; *op.r.*, right operculum; *par.sp.*, parasphenoid; *pt.*, pterygoid; *pt.tem.*, post-temporale; *s.op.*, sub-operculum; *tab.h.*, left tabular horn covered by a scale.



operculum. In the restoration (fig. 20, p. 186) we have assumed that the edge of the operculum overlapped the thin flange of the sub-operculum.

A bone labelled "subopercular?" was figured by Williston (1899, pl. 36, fig. 3). Though it is not much like our bone in shape, it may possibly be another form of it.

### *The Shoulder-Girdle.*

The first bone of the shoulder-girdle to be recognized was the clavicle, which was correctly described by Hancock and Atthey (1872). Since then the only investigator who has contributed usefully to what is known of this part of the skeleton is Miall, who not only published figures (rough and imperfect it is true) of the clavicle (1881, fig. 11, "coracoid"), but also figured the cleithrum (fig. 10, "scapula"), till then unknown, and made (pp. 296-7) some suggestions, now in the main confirmed, as to the way in which these bones were arranged in the girdle. Miall added another bone (fig. 9) as the "supra-scapula," but we can find nothing like it, and it certainly forms no part of the shoulder-girdle of *Sagenodus*. Fritsch discussed the shoulder-girdle at length, but the upshot, in the restoration which he gave in text-figures 158 and 160, p. 81, was anything but a happy application of his perfectly sound principle that *Ceratodus* was the best guide to the structure of "*Tenodus*."

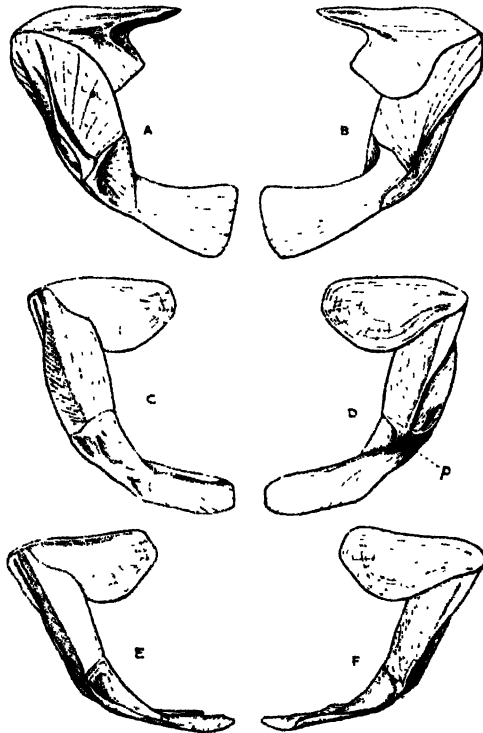
In the case of the shoulder-girdle, again, the figures here given (figs. 17, p. 182, and 19, p. 185) may largely take the place of a detailed description; and here again, as with the lower jaw, there is such a strong similarity to the corresponding parts in *Ceratodus* that the comparative outlines given in fig. 19 are practically self-explanatory.

The history of the discovery of the clavicle and cleithrum has been indicated above. The third bone, the post-temporal, has also long been known. It was fully discussed by both Miall and Fritsch, and on the strength of a certain resemblance to the combined squamosal and quadrate of *Ceratodus* they both figured it as the squamosal (Miall, fig. 6; Fritsch, text-fig. 153, p. 75). The clue to its real nature, as well as to the arrangement of the shoulder-girdle in general, was given by a fine specimen in the Atthey Collection, the pertinent portion of which is represented in fig. 18, p. 183. On its upper surface this specimen is chiefly noteworthy as being the only example we have met with which shows the operculum in its natural relation with the skull. It also shows the upper end of the right cleithrum from its outer aspect. On the under surface, as it was left by Atthey, the most prominent objects were the two clavicles, lying in nearly their natural position; the removal of masses of overlying scales has disclosed other structures which appear in our figure (fig. 18, B, p. 183). The right cleithrum and clavicle are in natural articulation. Underlying the left clavicle are the two post-temporals, the left one showing its strong anterior process projecting beyond the clavicle in front. Underlying the post-

temporals, again, is the parasphenoid, the backward prolongation of which is seen emerging from beneath them. The only other specimen we have seen showing the connection of cleithrum and clavicle is a detached example of these two bones in the Royal Scottish Museum.

A few remarks are called for on points of detail. As with other bones of the skeleton, those of the shoulder-girdle are variable, the cleithrum especially so. The inner face of the cleithrum is flattened; the outer is convexly thickened towards the upper end, and is strengthened by ribs of bone running

FIG. 19.



*Sagenodus* and *Ceratodus*. Comparison of shoulder-girdles.

A, B. Right side of shoulder-girdle of *Sagenodus*.

C, D. " " " *Ceratodus*, with the bones supposed flattened as are the fossil bones of *Sagenodus*.

E, F. Right side of shoulder-girdle of *Ceratodus*, with the bones in natural shape.

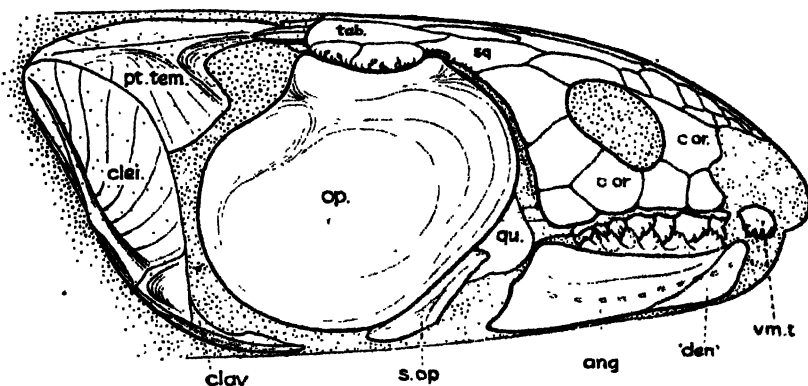
(Outer views on left, inner on right.)

upwards from the junction with the clavicle. Crushing has often resulted in these ribs being more or less plainly printed through on to the inner face. The cleithrum ends below in a transverse edge which is received into the head of the clavicle, and its hinder border is produced into a flattened and pointed process which fits into a slot in the back of the clavicle. The expanded upper end of the clavicle, with its deep pit for the attachment of

muscle, forms the "hatchet-shape" which Hancock and Atthey attributed to this bone.

Apart from the much greater strength of the bones in *Sagenodus*, the points of difference between its shoulder-girdle and that of *Ceratodus* are insignificant (fig. 19, p. 185). The strong forward process of the post-temporal in *Sigenodus* is plainly associated with the presence of a tabular horn, to which it was doubtless attached by its truncated point. In *Ceratodus* the post-temporal is merely attached to cartilage. The process of the cleithrum which serves to stiffen the union with the clavicle is represented in *Ceratodus* by a pyramidal point (fig. 19, p.), which if the bones were flattened would lie in the middle of the internal face instead of on the hinder border. In *Ceratodus* the muscle-pit in the head of the clavicle is divided by ridges into two or three pockets, but some of the clavicles of *Sagenodus* show an approach to the same condition. Finally, there can be no doubt that the blade of the clavicle was twisted as it is in *Ceratodus*, so that what appear in the flattened bones (fig. 19, A, B, p. 185) as its upper

FIG. 20.



*Sagenodus*. Restoration of skull and shoulder-girdle, in side view,  $\times \frac{1}{4}$ . *c.or.*, two of the circumorbitals; *vm.t.*, vomerrine "tooth." Each bone is founded on specimens in the Atthey Collection, but the association of the circumorbitals is conjectural.

and lower edges were in life the inner and outer edges respectively: while the surface represented in fig. 17, E, p. 182, and fig. 19, A, p. 185, is really the upper and internal surface, and that represented in fig. 17, F, and fig. 19, B, the lower and external. This will be understood from a comparison between the outline drawings in fig. 19, where the middle figures, C and D, show the shoulder-girdle of *Ceratodus* as it would appear if it were flattened out, like the bones of *Sagenodus*, by fossilization in shale. The actual specimens of the clavicle of *Sagenodus* show abundant evidence of having been strongly curved, for the flattening has produced a system of gaping cracks on the smooth inner face of the bones (fig. 17, G, p. 182). One

remarkable specimen occurring on a slab of shale in the Atthey Collection has, indeed, retained its original shape, though surrounded by other bones of *Sagenodus* which have all suffered the usual flattening. It should be added that the faces of the clavicle identified above as upper-and-internal and as lower-and-external have, as the figures show, all the character of internal and external faces respectively. Miall described and figured an articular area on the broad lower end of the clavicle, and he suggested that the two clavicles met each other at an acute angle in this articulation. Well-preserved examples, however, show no such articular area, nor would they fit together at all exactly by their ends. In all probability they were connected, as in *Ceratodus*, by an interclavicular cartilage.

We have nothing to add to what has already been published regarding the structure of the body, fins, and scales. There is every reason to suppose that these parts of *Sagenodus* are closely reproduced in the existing *Ceratodus*.

#### *The Species of Sagenodus.*

A glance at the portions of cranial roofs shown in outline in fig. 2, p. 165, will suggest that they represent more than one species of *Sagenodus*. At least one further species is certainly represented by the zoned and polished skull-bones found so abundantly in the Bohemian Gaskohle and in some numbers also at Newsham (*cf.* fig. 4. D, p. 168). But there is rarely anything distinctive about the teeth in the cases where it is possible to assign them with certainty to any particular pattern of skull, and there is little ground for attaching the slightest value to most of the specific names founded so freely on the teeth. Most parts of the skeleton, and especially perhaps the parasphenoids, the separate elements of the lower jaw, and the opercula, show varieties of pattern as important as those of the cranial roof and the teeth; and until the different patterns of all these parts have been studied and correlated there will be little use in applying specific names to *Sagenodus* at all. Such a study would be extremely difficult on account of the fragmentary nature of the evidence, and it might very possibly result in the conclusion that *Sagenodus* was, in its sphere of life, a dominant form in such a fluid evolutionary stage that it would be for the most part impossible to apply to it the ordinary conceptions of a species.

#### *Fritsch's figures of the Cranial Bones of Sagenodus.*

Fritsch's figures are beautifully drawn, and form a valuable atlas of the detached bones of *Sagenodus*, but the fact that so many of them are unidentified detracts from their usefulness. Some of these unidentified bones are named in the following list:—

*Plate 71 (Fauna der Gaskohle, vol. ii. part 2, 1899):* fig. 10, right intertemporal; fig. 11, right nasal.

*Plate 72, fig. 10, left "tabular."*

*Plate 74* includes a good selection of different forms of "parietals"; fig. 5, an extreme example of the rectangular type.

*Plate 75*, figs. 1-11, marginal ossicles, but including some ordinary roof-bones of small fishes, e. g. fig. 5, squamosal; 3, intertemporal; fig. 14, left intertemporal; 12, 19, circumorbitals; 20, l. "tabular"; 22, r. intertemporal; 24, l. squamosal; 25, l. frontal; 27, r. "tabular"; 28, r. squamosal, underside; 29, l. frontal, underside; 32, l. "tabular," underside, with one of its lateral bones; 33, nasal, underside; 34, fragment of squamosal; 37, marginal ossicles; 39, r. nasal.

*Plate 77*, fig. 17, "tabular."

*Plate 78*, fig. 6, post-temporal.

### CTENODUS, Agassiz.

The genera *Ctenodus* and *Sagenodus* were separated primarily on the characters of the tooth-plates, though when Owen first published the name *Sagenodus* he was under a misapprehension as to the nature of the tooth-section on which he founded it. Since the publication of Dr. Smith Woodward's "Catalogue of Fossil Fishes" (vol. ii., 1891), the name *Ctenodus* has been generally applied to tooth-plates with about 12 or more ridges, roughly parallel, as contrasted with the others (*Sagenodus*) having fewer, usually 6 or 7, ridges, with a strongly-marked radial arrangement. If this were the only distinction between the two genera it would be difficult to maintain, since tooth-plates of intermediate character occur in the Lower Carboniferous of Edinburgh. There are, however, many other distinctive characters independent of the difference in the teeth; and in spite of a general resemblance which shows the two genera to be nearly related, the additions which we are able to make to what was known of each of them tend still further to justify their separation.

*Sagenodus* having been dealt with already, *Ctenodus* can be sufficiently described, with the aid of figures, on brief and comparative lines.

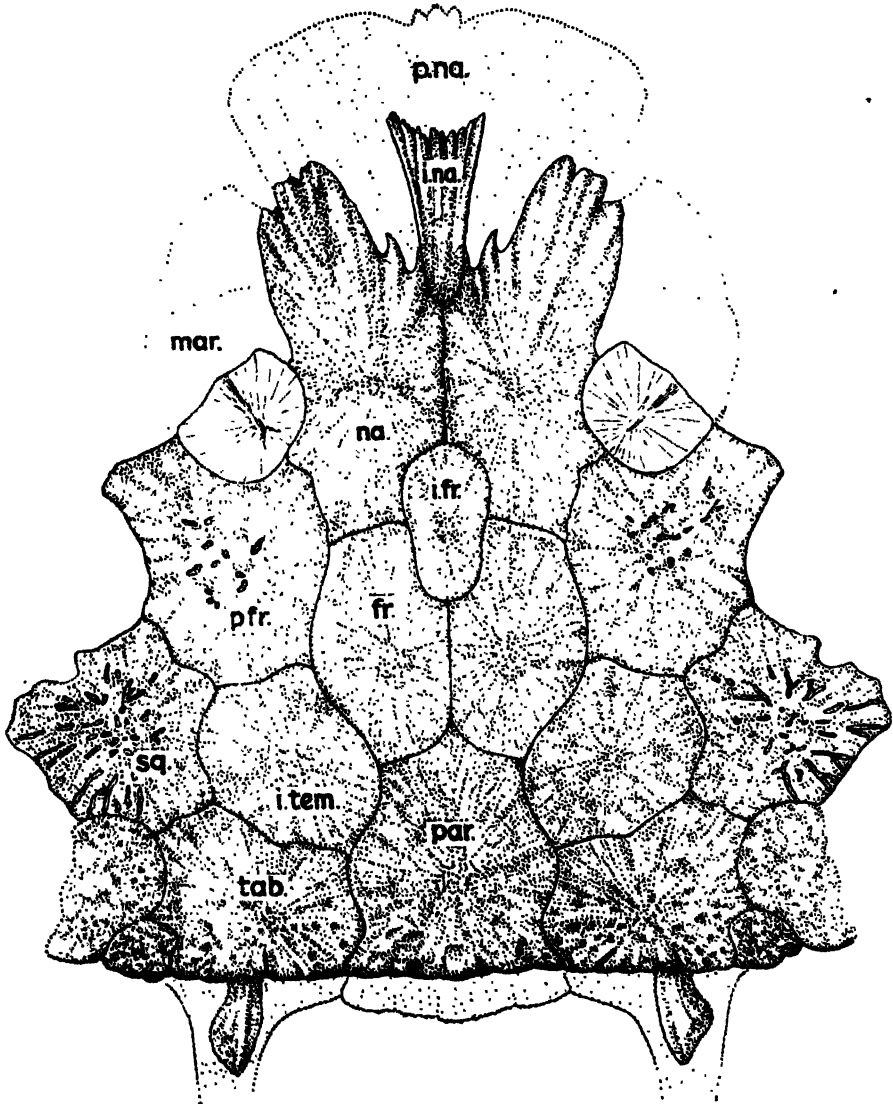
In most or all of the beds and horizons from which we have had material for examination, remains of *Ctenodus* are much less abundant than those of *Sagenodus*, and there is consequently more difficulty in ascertaining its skeletal structure with completeness. In particular there is in the collections, up to the present, an almost entire absence of specimens such as were of the greatest help in the case of *Sagenodus*, namely slabs bearing the scattered remains of some considerable part of an individual fish. We have never yet, for example, seen any considerable part of the shoulder-girdle of *Ctenodus* in association with other portions of its skeleton, and the bones which we take to be those of its shoulder-girdle are assigned to it without absolute proof, though on strong grounds of probability.

The fishes of the genus *Ctenodus* were of decidedly larger average size than those comprised in *Sagenodus*. Nine or ten inches is a usual length for skulls of *Ctenodus*, as compared with five or six inches for skulls of *Sagenodus*.

*The Roof of the Skull.*

The skull of *Ctenodus* was ossified to the same extent as that of *Sagenodus*, and similarly shows no trace of ossification of the neural chondrocranium. A comparison of fig. 1, p. 164. and fig. 21, below, will show that the skull-roofs of the two genera differ considerably—more, in fact, than any other

FIG. 21.



*Ctenodus cristatus*. Cranial roof. *fr.*, frontal; *i.fr.*, interfrontal; *i.na.*, internasal; *i.tem.*, intertemporal; *mar.*, marginal bones; *par.*, "parietal" (=parietal + dermo-supra-occipital); *p.fr.*, pre- or post-frontal; *p.na.*, prenasal; *sq.*, "squamosal"; *tab.*, "tabular" (=tabular + supratemporal).  $\times$  about  $\frac{1}{4}$ .

part of the skeleton,—but that the general plan is the same. In the posterior region the correspondence is very close. The main points of difference may be broadly stated thus: in *Ctenodus* the two median bones (*par.* and *i.fr.*) are much smaller and the bones of the nasal region much larger, while there are two pairs of bones in the frontal region instead of only one. As far as its skull-roof is concerned, *Ctenodus*, being nearer to the Devonian *Dipterus*, is presumably the more primitive; and we may usefully think of the skull-roof of *Sagenodus* as being derived from that of *Ctenodus* by a great reduction of the snout region together with an increase in size and eventual meeting of the two median bones, both processes together resulting in the compression, and finally in the fusion, of the frontal and post-frontal on each side.

As long ago as 1872 Hancock and Atthey correctly pointed out, as one of the main features distinguishing the skull of *Ctenodus* proper from that of *Sagenodus* (“*Ctenodus obliquus*”), that the two median bones of the roof are separated and that the hinder one consequently has a pointed instead of a concave anterior margin. Dr. Smith Woodward (1891, p. 250) refers to the same distinction when he states that there are “two median occipital plates” in *Sagenodus* and only one in *Ctenodus*. He also gives (pp. 252-3) the only extended description hitherto published of the skull-roof in *Ctenodus*, but the specimen on which he founded it (B.M., P. 5031), figured in pl. 4. vol. ii., of his catalogue, is not well preserved; it shows for the most part impressions of the under surface of the bones, and their outlines are too indistinct for accurate representation. The same specimen was roughly figured by Fritsch (1889, text-fig. 156), but as he failed even to identify the middle line, his observations on it (p. 98) were not helpful.

Another specimen (now in the British Museum, P. 7300) was also roughly figured by Fritsch in his text-figure 155, and is represented in outline in our fig. 23, A, p. 192. It is chiefly remarkable as showing a considerable ossification in advance of the nasals, in the form of a radially-ribbed fan. Fragments of a similar fan in the Atthey Collection are shown in fig. 22, p. 191. Except at their outer edge, the bone composing them is as thick as that of any other part of the cranial roof.

The presence of an internasal is a further point of distinction from *Sagenodus*. The form of internasal shown in fig. 21, p. 189, of which two specimens are known, is possibly characteristic of *Ctenodus cristatus*. The form figured in B, fig. 23, p. 192, may similarly be characteristic of “*C. interruptus*.”

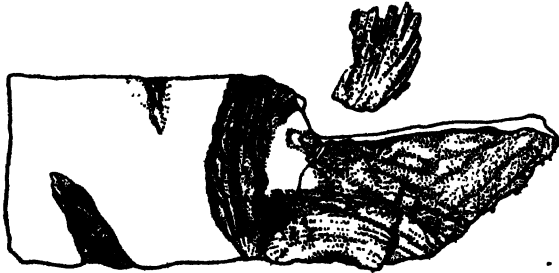
The bones of the roof proper in *Ctenodus* seem to be about as variable in shape as in *Sagenodus*. The specimens we have examined show that the most variable elements are the interfrontal, internasal, and post-frontal (compare fig. 21, p. 189, with the outlines in fig. 23, p. 192). From the condition of the available specimens it would appear that the elements of the cranial roof of *Ctenodus* were more firmly united than those of *Sagenodus*,

for they very rarely occur as isolated bones, whereas isolated roof-bones of *Sagenodus* are abundant.

The circumorbitals of *Ctenodus* are shown only in one specimen among our material, and this is represented in outline in fig. 23, B, p. 192. In number and in general arrangement they appear to differ little from the circumorbitals of *Sagenodus*, except that a small bone, partially embraced by the squamosal and post-frontal, occurs between them and the bones which actually enter into the orbit. This, however, may be an arrangement peculiar to "*Ctenodus interruptus*."

In addition to the circumorbitals there are, as in *Sagenodus*, some bones filling in the space to the outer side of the nasals. They are not completely shown in any specimen that we have seen, but they obviously vary a good deal in shape (*mar.*, fig. 21, p. 189, and fig. 23, p. 192). The single one shown in fig. 21 is represented as an impression of the underside, which is all that had been seen of it when the figure was drawn.

FIG. 22.

Fragments of the prenasal fan of *Ctenodus*,  $\times 4$ .

### *The Palate.*

A comparison of fig. 10, p. 176, and fig. 26, p. 195, will show the close resemblance between the bones of the palate in *Ctenodus* and *Sagenodus*. The tooth-plate of *Ctenodus* is larger (fig. 8, p. 173), the pterygoid behind it is of rather more slender form, and the parasphenoid (fig. 25, p. 194) has a more prominent median ridge on the buccal face of the lozenge. The shaft of the parasphenoid is more abruptly expanded, and shows a pair of pits close behind the apex of the lozenge. On the cranial surface the ridges and grooves of the shaft are much more numerous than in *Sagenodus* (*cf.* fig. 9, C, p. 174), and are continued forward to the centre of the lozenge, where they nearly meet the corresponding ridges from the anterior process.

In the larger parasphenoids, some of which are nearly a foot in length, the median ridge of the lozenge is swollen and club-shaped (fig. 26, p. 195), and it seems to be usual for the right-hand pit of the pair behind it to communicate directly with the central groove of the shaft, as shown in fig. 25, C, p. 194. The appearance is suggestive of the crossing of a pair of longitudinal

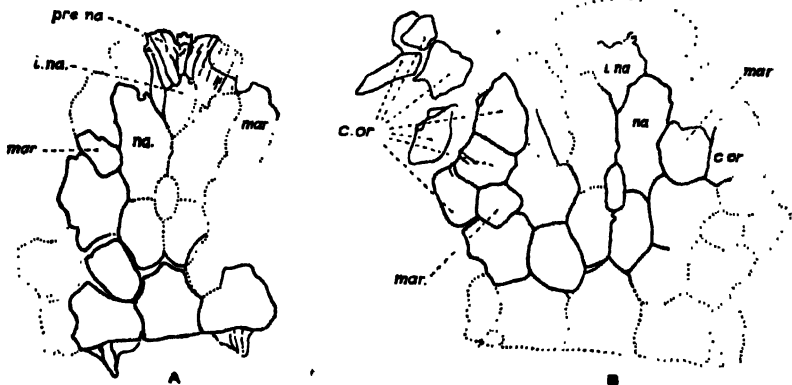


muscles. The species "*Ctenodus interruptus*" from the Lower Carboniferous, though proved by its cranial roof (fig. 23, B, p. 192) to be a true *Ctenodus*, has a palate and tooth-plates which in all respects much more nearly resemble those of a *Sagenodus* (see fig. 24, p. 193).

### *The Quadrate.*

The bone which we take to be the quadrate of *Ctenodus* is represented in fig. 11, A and B, p. 177. There are two or three examples of it in the Atthey Collection, and one of them was labelled by Atthey himself "*Ctenodus*, os quadratum." Fig. 11, p. 177, shows sufficiently how it differs from the quadrate of *Sagenodus*, the most striking difference being the much smaller development of the longitudinal ridge on the inner side.

FIG. 23.



C TENODUS.

- A. Cranial roof of a specimen of *C. cristatus* from Longton, Staffs. B.M.N.H. 7300.  
 B. Cranial roof of "*Ctenodus interruptus*, Barkas," Dunnet shale, Straiton, Midlothian. 1895/155/12, R.S.M. Of importance as being the most perfect cranial roof of this species existing, and showing more connected circumorbitals than any other specimen of *Ctenodus* known. The detached circumorbitals are preserved on the counter slab, and really partially underlie those which are attached to the roof. A palatal tooth, omitted from the figure for the sake of clearness, establishes the specific identity of the specimen.  $\times \frac{1}{2}$ .

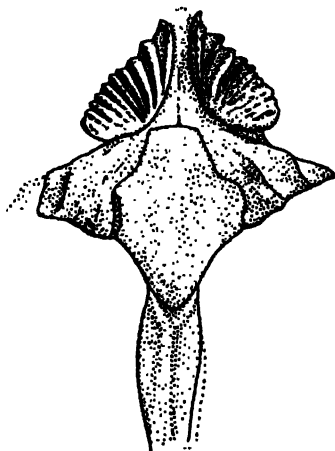
### *The Lower Jaw.*

Remains of the lower jaw of *Ctenodus* are scarce, but specimens from Newsham in the Atthey Collection and in the British Museum make it possible to reconstruct the jaw as has been done in fig. 27, p. 196. In general plan, and to a large extent in detail as well, it agrees with the jaws of *Sagenodus* (fig. 12, p. 178) and *Ceratodus* (fig. 13, p. 179). The chief difference is in the greater breadth of the tooth-plates and, correlated with it, the greater width of the "dentaries." Instead of coming almost or quite to a point in front, as do the "dentaries" of *Sagenodus*, those of *Ctenodus* have a wide anterior edge and carry the front ends of the angulars some

distance outwards from the middle line. Another result of the greater breadth of the tooth-plate is that it is supported posteriorly, not, as in *Sagenodus*, by a bracket on the inner face of the upper border of the angular, but by a pocket in the same position on the outer face (see fig. 27, E, p. 196). The "splenial" is a much weaker bone than in either *Sagenodus* or *Ceratodus*; its symphysial end is fairly strong and some part of it is commonly to be seen projecting in front of the mandibular teeth, but behind the symphysis it is so thin that it has usually been folded or crumpled beneath the tooth-plate in fossilization.

The posterior edge of the "dentaries" is thickened and polished precisely as in *Sagenodus*, and no doubt there were gular plates fitting against it, but so far we have not found any bones that we could identify as gulars of *Ctenodus*.

FIG. 24.



"*Ctenodus interruptus*, Barkas."

Pterygoid with teeth and parasphenoid, oral aspect,  $\times \frac{1}{2}$ .

Oil shale of Broxburn, Midlothian (1902-73, R.S.M.).

The left pterygoid is entirely, the right very nearly in natural articulation with the parasphenoid.

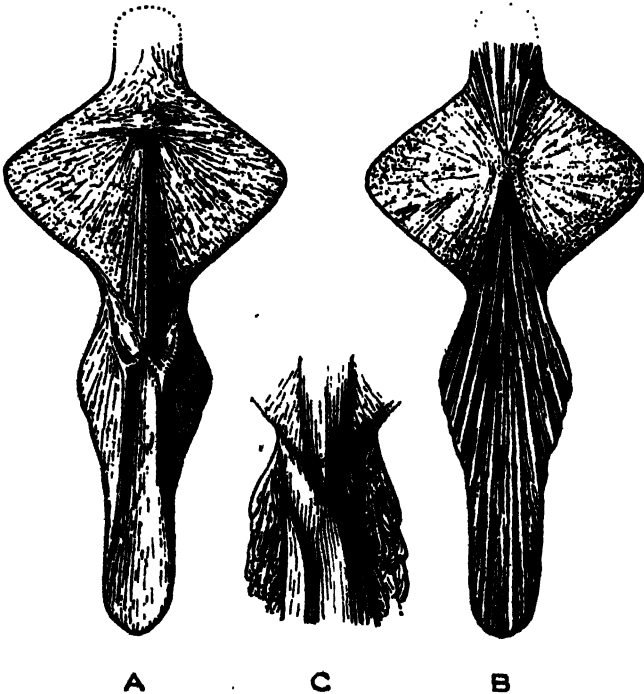
The *Operculum* seems to have been exactly like that of *Sagenodus*. Several specimens in the Atthey Collection are too large for any known skull of *Sagenodus*, and these at least presumably belong to *Ctenodus*; but, apart from maximum size, we can point to no definite character by which opercula of the two genera may be distinguished. A sub-operculum was doubtless present, but we have not yet succeeded in identifying it.

#### *The Shoulder-Girdle.*

As already stated, we have never yet seen well-preserved bones of the shoulder-girdle associated with undoubted remains of *Ctenodus*.

Nevertheless we have little hesitation in regarding the bones shown in fig. 28, p. 197, as the cleithrum and clavicle. Both are well represented in the Atthey Collection; from comparison with the corresponding bones of *Sagenodus* (fig. 17, p. 182), there can be no doubt that they are the cleithrum and clavicle of a Dipnoan; and both reach too large a size to belong to any known form of *Sagenodus*. The cleithrum (fig. 28, A, p. 197) is found up to 7 inches (33 cm.) in length, the clavicle to at least 6 inches (30 cm.). The cleithrum differs from that of *Sagenodus* chiefly in having its hinder half (the upper part in A, fig. 28, p. 197) greatly thickened instead of

FIG. 25.

*Ctenodus cristatus*. Parnsphenoid.

A. Buccal aspect. B. Cranial aspect.

C. Junction of disc and shaft in large examples.

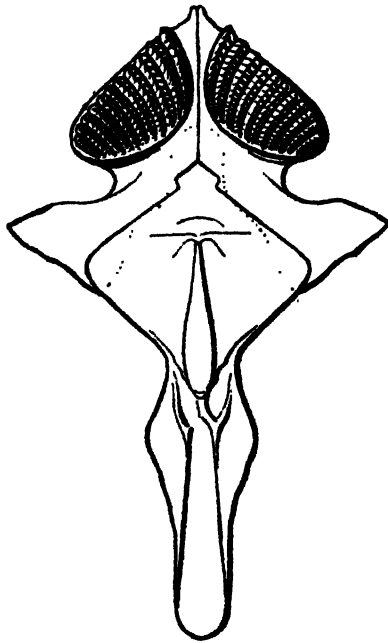
being strengthened by longitudinal ribs. Moreover, on its outer side this thickened portion has the character of a superficial bone, as though it had come to the surface under the skin behind the operculum as in *Dipterus*, instead of being buried in muscle as in *Ceratodus*, and as it presumably was in *Sagenodus* too.

The clavicle (fig. 28, B, C, p. 197), though it has the same essential structure as that of *Sagenodus*, differs from it in having a longer articular head and a narrower and stouter shaft. We have found no specimens with

perfectly preserved heads, and our figure is therefore less complete in that part than the corresponding figures for *Sagenodus* (fig. 17, p. 182). Miall had apparently seen examples, though still more imperfect ones, of the same bone (1880, fig. 12), and he evidently suspected that it belonged to the shoulder-girdle of *Ctenodus* proper, for he labels it "*Ctenodus cristatus* or *tuberculatus*? Coracoid."

We have found one or two bones which may prove to be post-temporals of *Ctenodus*, but have not been able yet to identify them with any approach to certainty.

FIG. 26.



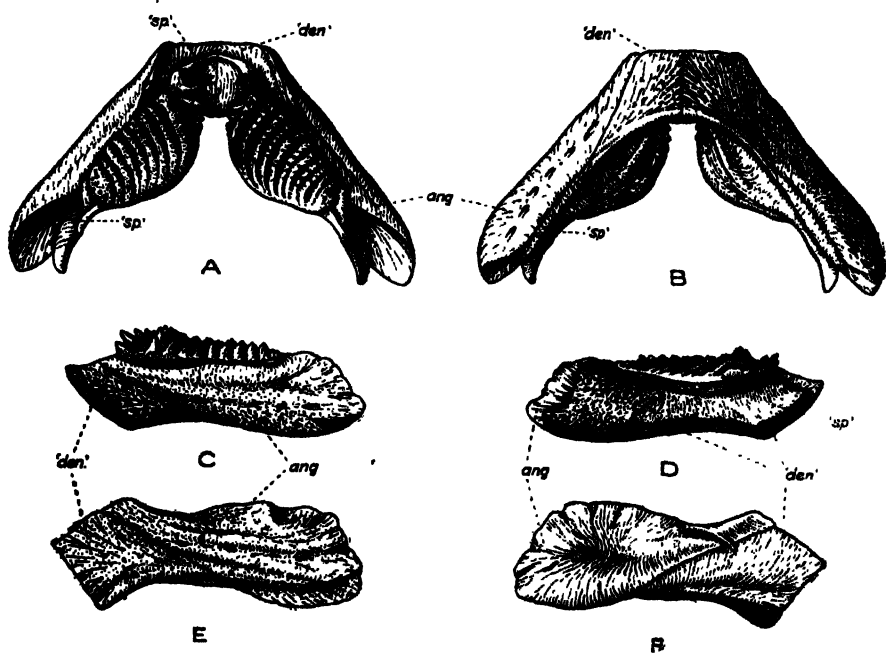
*Ctenodus cristatus*. Pterygoids with their teeth, in natural articulation with the parasphenoid. Quadrate rami shown flattened into the same plane as the parasphenoid.  $\times \frac{1}{2}$ .

### *The Species of Ctenodus.*

Dr. Smith Woodward was probably well advised in reducing the specific names *tuberculatus*, *ovatus*, etc., to the position of synonyms of *C. cristatus*. The tooth-plates of *Ctenodus*, on which all the specific names have been founded, are if anything more variable even than those of *Sagenodus*. They are, in fact, likely to be so, since they represent a departure from the standard Dipnoan type of dentition as established in *Dipterus* and carried on in *Sagenodus* and *Ceratodus*. A perfectly distinct species, however, is the

extremely interesting early form which we, following Traquair's usage, have referred to as "*Ctenodus interruptus*, Barkas." (If Dr. Smith Woodward's diagnosis of this species, 'Catalogue of Fossil Fishes,' part ii. p. 254, accurately represents Barkas's intention in founding the species, the name cannot properly be applied to the specimens in the Royal Scottish Museum which Traquair referred to it.) The *Sagenodus*-like teeth of this fish (fig. 24, p. 193) are in the strongest contrast with those of the latest known species, *C. murchisoni*, Ward, from the Upper Coal Measures, which have about twenty practically parallel ridges.

FIG. 27.



*Ctenodus*. Lower jaw,  $\times \frac{1}{2}$ .

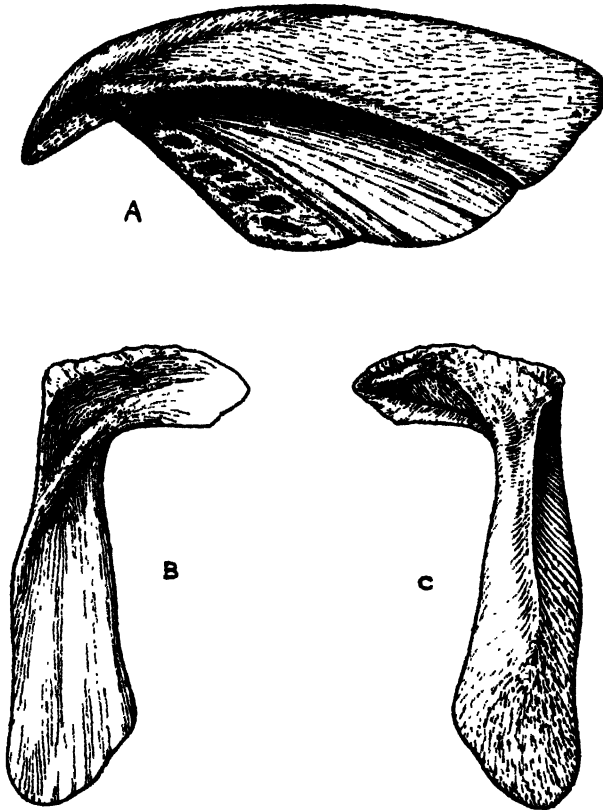
- A. Reconstruction of lower jaw, from buccal aspect.
  - B. Ventral aspect of the same.
  - C. Left ramus, outer aspect.
  - D. „ inner aspect.
  - E. An angular and dentary in natural articulation. From two specimens, in the Atthey Collection and the British Museum respectively.
  - F. The same, inner surface. From the Atthey specimen.
- (Compare figs. 11 and 12, pp. 178, 179.)

Fritsch's *Ctenodus tardus* from the Brandschiefer (Lower Permian) of Bohemia, represented in his Taf. 80 b, is apparently a Dipnoan; but if his drawing of the bones of the skull-roof is at all accurate, it was certainly neither a *Ctenodus* nor a *Sagenodus*.

*Ctenodus*, *Sagenodus*, and *Ceratodus*.

The close correspondence which has been traced in the structure of these three genera, notably as regards the palate, the lower jaw and the shoulder-girdle, leaves no doubt as to their near affinity. The structure of the skull-roof, if followed through the same three fishes, shows less constancy; on the

FIG. 28.



*Ctenodus*? A. Cleithrum. B, C. Clavicle, upper and lower surfaces.  
Both bones are represented by numerous specimens in the Atthey Collection.

other hand, it shows an interesting progressive change, starting from the pattern first established in *Dipterus platycephalus*. The change consists in the expansion, at the expense of the surrounding bones, of the median "parietal" and interfrontal, together with the reduction of the bones of the snout region (nasals and prenasals). From *Dipterus* to *Ctenodus* the change, though obvious, is not great. From *Ctenodus* to *Sagenodus* it is in both respects very marked; in *Ceratodus* it has been carried to an extreme, for

FIG. 29 A.

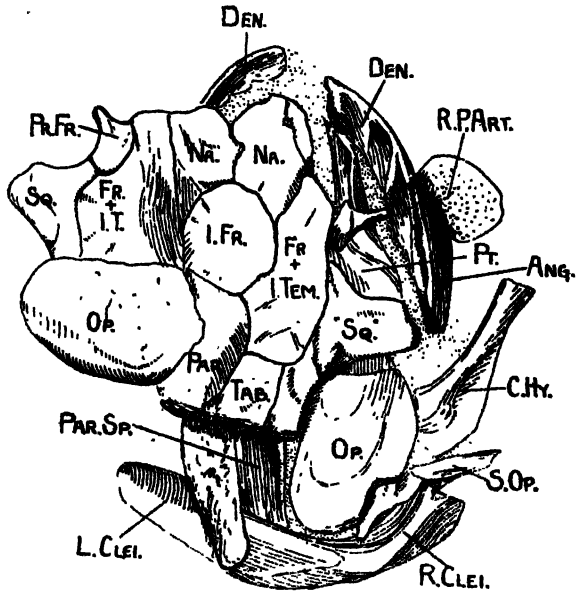
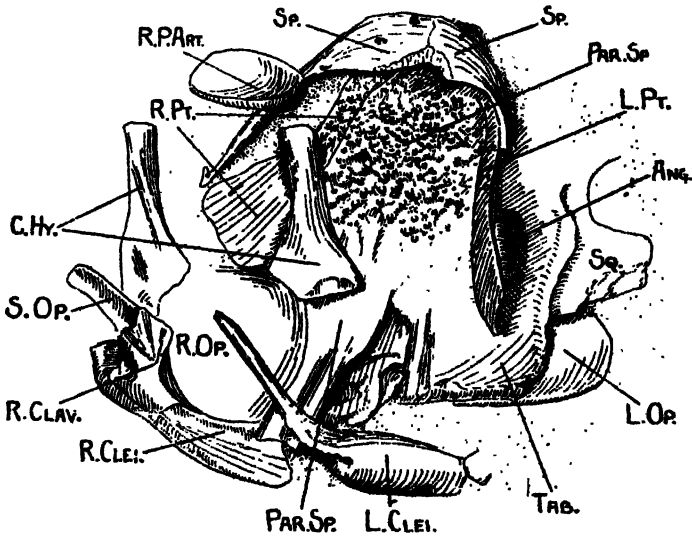


FIG. 29 B.



*Conchopoma gadiformis*, Kner. Drawn from gelatine casts from the two halves of a specimen in the Royal Scottish Museum.  $\times 1$ .

- A. Dorsal surface of head. ANG., angular; C.HY., ceratohyal; DEN., dentary; FR. + I.T., frontal + intertemporal; I.FR., interfrontal; L.CLEI., left cleithrum; NA., nasal; OP., operculum; PA., parietal + dermo-supraoccipital; PAR.SP., parasphenoid; PR.FR., prefrontal; PT., pterygoid; R.CLEI., right cleithrum; R.PART., right pre-articular; S.OP., sub-operculum; SQ., "squamosal"; TAB., tabular + supra-temporal.
- B. Ventral surface of head. Reference letters as before, with L.PR., left pterygoid; L.OP., left operculum; R.CLAV., right clavicle; R.OP., right operculum; R.PT., right pterygoid. The mass of bone between PAR.SP. and L.CLEI. is the exoccipital.

the bones of the snout region have almost or quite disappeared, and the "parietal" and interfrontal cover the whole median tract of the top of the head.

The compression of the lateral bones of the skull-roof brought about by this expansion of two of the median bones appears to have resulted in corresponding degrees of disappearance or fusion. Thus in *Sagenodus* there is only one pair of bones in the frontal region as compared with two in *Ctenodus* and three or more in *Dipterus platycephalus*. *Ceratodus* is extreme in this respect as in the others: all the bones of the frontal, temporal, and tabular regions on each side seem to be represented as a rule by a single ossification.

*Conchopoma*, another Dipnoan appearing late in order of time and described below, furnishes an interesting parallel to *Ceratodus*. Though none of the processes have gone as far as in *Ceratodus forsteri*, yet the two median bones are greatly expanded, the bones of the snout much reduced, and those of the lateral part of the roof extensively fused.

Several of the minor characters of the bones of the head in *Ceratodus* as compared with those of *Sagenodus* are plainly correlated with one another. The side-to-side arching of the skull-roof, bringing the squamosal region far down on the side of the head, is connected with the reduction in size of the operculum, and also with the shortening of the quadrate.

#### CONCHOPOMA GADIFORMIS, Kner.

The rare fish from the Lebach Shales (uppermost Carboniferous) of Saarbruck, called *Conchopoma gadiformis* by Kner, has never been at all adequately described. There is in Edinburgh a very large individual, preserved in an ironstone nodule, which makes the structure very nearly completely known. It was prepared by softening the already rotted bones with dilute acid and removing the residue by brushing. Casts from the moulds so left show all surface details extremely well.

The general morphology will be obvious from fig. 29, p. 198. The skull has the usual Dipnoan structure of an extensive cartilaginous neural cranium, which seems to have been considerably ossified in the exoccipital region. The head is roofed by a continuous shield of membrane bones, which, although now flat, seems from its cracked condition to have been originally considerably curved. This shield consists posteriorly of a row of three bones, of which the median "parietal" is longer than the lateral tabular. The "parietal" has a low median ridge on its visceral surface: the "tabulars" are concave ventrally and now no signs of attachments.

The "parietal" articulates with a median interfrontal, and these two bones have long lateral attachments to the very large bones which include the



frontals; these bones articulate with the "tabular" behind, and seem just to reach the free anterior edge of the shield.

The lateral edge of the "tabular" and "frontal" is attached to a series of bones, the posterior two? of which are narrow and form that margin of the skull to which the operculum is attached; they are imperfectly shown from the dorsal surface on the right, and are absent on the left side. Immediately in advance of these is a very large element forming an outstanding wing behind the orbit. This extends forward and just touches a much smaller bone, which forms the anterior and upper quadrant of the orbital margin.

The dorsal shield is completed by a pair of bones which articulate with the front margins of the frontals and interfrontal.

There are no traces of other circumorbitals or of premaxillæ.

The palate presents an interesting modification of the Dipnoan type. The parasphenoid has a long, slender dorsally channelled stem, which expands into a broad, shovel-shaped, flat bony plate extending forward as far as the symphysis of the lower jaw. This region of the parasphenoid is covered with teeth, small and very closely packed anteriorly, somewhat larger and more scattered posteriorly. These teeth are quite irregular in arrangement, but little groups of two or three of them are often supported on a common raised base; anteriorly where the teeth become inconspicuous the bases may persist as short curved ridges.

The pterygoid on the left side seems to retain its natural position, standing up nearly at right-angles to the palate.

The bone is very narrow anteriorly, forming a border to the great parasphenoid and having irregularly arranged small teeth. Posteriorly the bone becomes converted into a deep thin flange, which was formerly applied to the quadrate and stands nearly at right-angles to the palate.

The operculum has long been known as a concavo-convex bone with an umbo at its antero-dorsal corner. This specimen shows a small bone on the right side which seems to be a sub-operculum, because of its resemblance to that bone in *Dipterus* and *Sagenodus*.

The structure of the lower jaw is not satisfactorily shown. There is a powerful symphysis formed by bones of the outer surface homologous with the "dentaries" of *Sagenodus*, but possibly including true dentaries in addition.

There is a large angular of whose structure nothing can be said. Although this lower jaw lies in its natural position and the mouth is closed, no trace of the bones usually called splenial can be seen in it. There is, however, a strange tooth-bearing bone with a concave visceral surface lying displaced in contact with the right ramus, which apparently can only be this element. It differs from the corresponding bone in all other Dipnoi in lacking a posterior flange passing back to the articular and an anterior symphysis. The two

ceratohyals are well shown; they exactly resemble the corresponding bones in *Ceratodus*.

The shoulder-girdle is remarkable for the very small relative size of the clavicle.

The cleithrum is a large bone of much greater width than is shown in the figures, where part of it is hidden by matrix in each case. The upper end is comparatively narrow, and is seen to be covered by a very badly preserved bone, no doubt the supra-cleithrum. The inner surface is concave, the outer flat with a turned-in anterior margin; it has a depressed area for the hinder edge of the operculum. The lower end of the cleithrum turns forward and is largely covered by the sub-operculum, appearing behind that bone only as a narrow strip.

The clavicle is displaced and shown only from its outer surface. It is extremely short, attached to the cleithrum by a deeply recessed triangular area on its outer surface, and widening both ways ventrally.

The neural arches are thoroughly ossified anteriorly, although there are no ossifications in the notochordal region. The anterior neural spines are separately ossified from their arches. The ribs are slender, well curved and with slightly thickened heads.

The structure of the median fins is already familiar; there is a continuous fin agreeing exactly in structure and distribution with that of *Ceratodus*.

The pectoral fins are shown by the Edinburgh specimen to be large, typical biserial archipterygia, the axis being entirely unossified, whilst the radials of both series have short, hollow ossifications. There are very well-developed camptotrichia which do not extend in to overlap the ossified radials.

The structure of the pelvic fins is not so clearly shown, but they obviously agree in general with the pectoral fins, and are nearly as large.

The scales are not very well shown; they are thin, of considerable size, and marked with very delicate concentric rings of growth. It is impossible to say how far forward they extended.

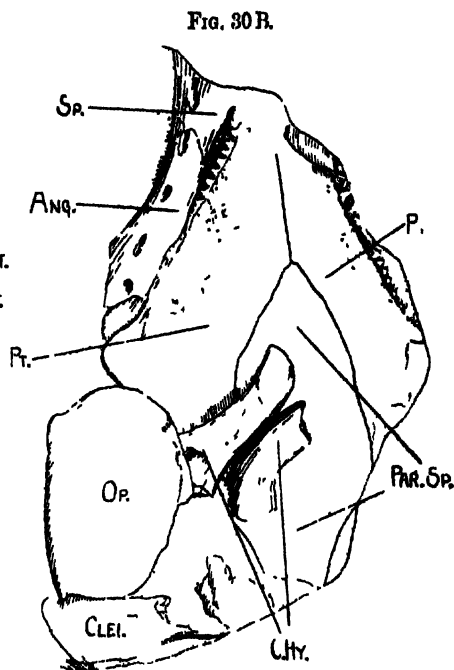
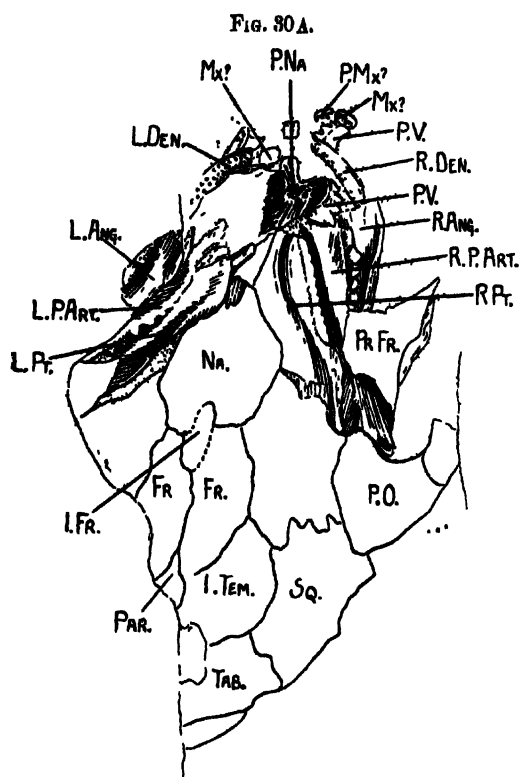
*Conchopoma* must have been extremely like *Ceratodus* in proportions and general build, although the head may have been slightly lower posteriorly.

#### URONEMUS SPLENDENS (Traquair).

The genus *Uronemus* was founded by Agassiz for some small fish from the Burdiehouse Limestone, which have a continuous median fin and an apparently diphyccercal tail. To this genus Dr. Traquair referred some remains from the Lower Carboniferous, No. 2 Ironstone, Loanhead, Midlothian, which show many details of skull structure. Beyond stating that these specimens show a skull-roof like that of *Ctenodus* and prove that the pterygoids and "splenials" bear a single series of large, compressed, low, conical teeth in addition to a granulation of small denticles, there being no

dental plates of a normal Dipnoan structure, he gave no further account of them, and never published any figures in illustration of his description. In 1891 Dr. Smith Woodward gave a figure of an isolated "splenial," since when no further details have been published.

The types are in the Royal Scottish Museum, and between them make the structure nearly completely known.



*Uronemus splendens*, Traq. Drawn from plasticene squeezes of a specimen in the Royal Scottish Museum.  $\times 1$ .

- A. Dorsal surface of head. Fr., frontal; I.Fr., interfrontal; I.TEM., intertemporal; L.ANG., left angular; L.DEN., left dentary; L.P.ART., left pre-articular; L.Pt., left pterygoid; Mx.?, maxilla; Na., nasal; P.O., post-orbital; P.V., prevomer; Pr.Fr., prefrontal; P.Mx.?, premaxilla; PAR., parietal; R.ANG., right angular; R.DEN., right dentary; R.P.ART., right pre-articular; R.Pt., right pterygoid.
- B. Ventral surface of head. Reference letters as before, with C.Hy., ceratohyal; CLEI., cleithrum; OR., operculum; PAR.SP., parasphenoid.

The best specimen is a nearly complete small fish, preserved mainly as an impression in slab and counter slab.

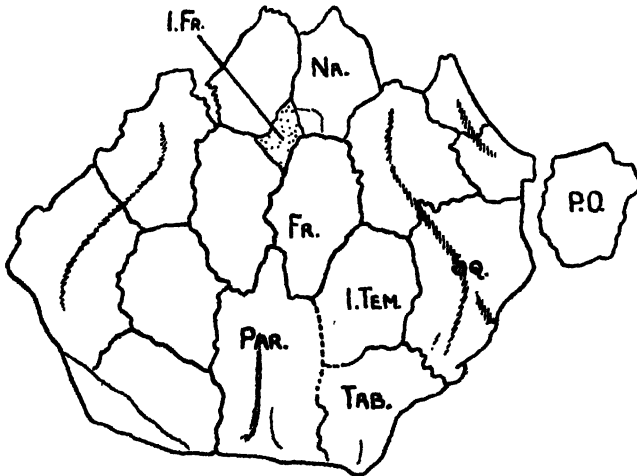
I have prepared it by removing the scanty remains of bone from the impressions, and studied it in plasticene squeezes, which reproduce all surface

details with great perfection. Other specimens show the cranial roof from the visceral surface.

The cranial roof consists of a series of bones arranged very nearly as in *Ctenodus*, but the three nearly complete examples in Edinburgh differ in details. There is a posterior row of three bones, a median "parietal," which supports a pair of frontals, and lateral tabulars which are shorter than the "parietal" and are continued forward by intertemporals.

The frontals are separated anteriorly by a small interfrontal, but support a pair of nasals in two specimens and only a single median nasal in the skeleton. Finally, in this specimen the skull-roof is completed by a small median prenasal with a notched anterior border.

FIG. 31.



*Uronemus splendens*, Traq. Roof of the skull, seen from the ventral surface.  $\times 3$ .

Fr., frontal; I.Fr., interfrontal; I.TEm., intertemporal; Na., nasal; P.O., post-orbital; PAr., parietal; Sq., "squamosal"; TAB., "tabular."

The intertemporal and tabular articulate with a large squamosal, there being no evidence of the presence of the two small elements which in most Dipnoi appear on the margin of the shield bordering the tabular and squamosal.

The intertemporal is continued forward by a large post-frontal, which itself supported another element, which although now lost in every specimen cannot have entered the orbital margin.

Four circumorbital bones are preserved in the skeleton; probably one more was originally present. The three specimens which show that region differ considerably in the details of these circumorbitals, which articulate with the squamosal and post-frontal. All the bones of the skull-roof bear a crisply-marked fine ornament of ridges and pits, which in general radiate from the

centre of the bone. This ornament much resembles that of *Stegocephalian* skulls, and is unique amongst *Dipnoi*.

The palate is beautifully shown in the skeleton. The parasphenoid has a wide but incompletely preserved stem, which expands into an elongated but relatively very narrow lozenge, with the margin of which the pterygoids articulate.

The pterygoids cover a very large area, meeting one another in a long symphysis in front of the parasphenoid and passing out to the lateral margins, which are quite straight and make an acute angle with one another. The hinder end of the pterygoid is widened, is attached to the parasphenoid by a very long suture, and produced into a rounded corner in the quadrate region.

The dentition of each pterygoid consists of a marginal row of large, compressed, conical teeth and of a very large number of small, almost hemispherical denticles covering a narrow area within the margin. These denticles are rather regularly arranged in a series of straight lines, running parallel to one another from caudal and lateral to cranial and mesial; that is, they do not agree with the normal direction of teeth-rows seen in the pterygoids of *Dipterus* and *Sagenodus*.

The two prevomers of the skeleton are preserved; each consists of a bone with a cylindrical notch on the dorsal surface, which supports a row of four denticles exactly similar to those of the "splenial."

There are in the skeleton three small bones, each bearing small, elongated teeth; two of them lie in close association with a prevomer: it is certain that they are not lower jaw elements, and the conclusion seems irresistible that they are premaxillæ and maxillæ corresponding to those found by Watson and Day in *Phaneropleuron*.

The two rami of the lower jaw are separable at the symphysis, and each consists of at least three, almost certainly of four, bones.

The angular is a large bone exactly like that of *Ctenodus* in shape and bearing a similar row of sensory pits. It articulates by a fine suture with a splenial (dentary of *Ceratodus*), which presumably extended to the symphysis.

There is a rather large dentary, whose distinctness from the splenial cannot be proved, which bears an irregular strip of crowded small denticles. The prearticular (splenial of *Ceratodus*) extends from the articular region, toward and probably up to the symphysis; it bears only a single series of teeth on its upper edge, which bite outside and are exactly similar to the marginal teeth of the pterygoid.

The opercular apparatus seems to consist only of a large oval operculum, agreeing closely in shape with that of *Sagenodus*.

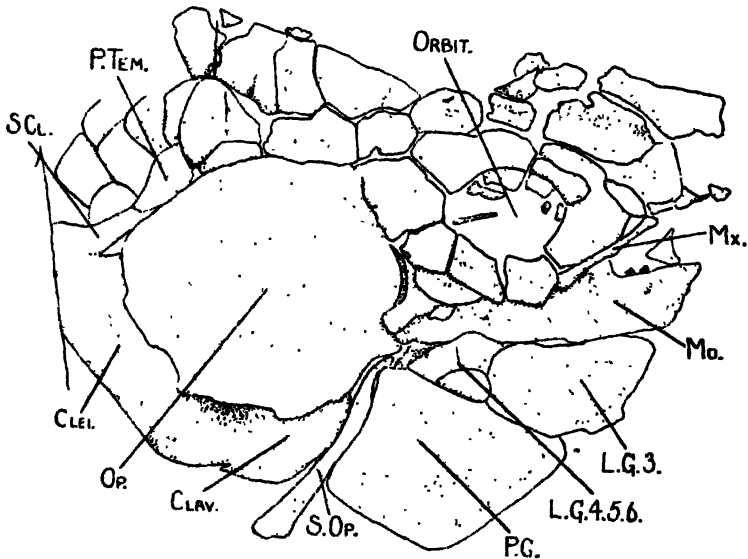
There are a pair of badly-preserved ceratohyals, agreeing closely with those of *Ceratodus*.

**DIPTERUS VALENCIENNESI, Sedg. & Murch.**

*Dipterus valenciennesi* is a small fish, found very abundantly in the western end of the mainland of Orkney and at Banniskirk, Achanarras, and other localities in Caithness, and, except at Edderton Burn, only very rarely in the nodules of the Moray Firth.

It was distinguished from the more recent *D. platycephalus* by Pander on account of its smaller size, lack of shiny surface on the cranial bones and scales, and lack of well-ossified anterior ends of the skull and mandible. Dr. Traquair, presumably because large specimens which in these characters agree with *D. platycephalus* do occur at Achanarras, Gamrie, and Cromarty and in association with a small fish which he regarded as *D. valenciennesi* at

FIG. 32.



*Dipterus valenciennesi*, Sedg. & Murch. Right lateral aspect of a crushed head.  $\times 2$ .

From a specimen in D. M. S. Watson's collection.

CLAV., clavicle; CLEI., cleithrum; L.G. 3-6, lateral gulars, nos. 3-6; Mo., mandible; Mx., maxilla; OP., operculum; P.G., principal gular; P.TEM., post-temporal; S.CL., supra-cleithrum; S.OP., sub-operculum.

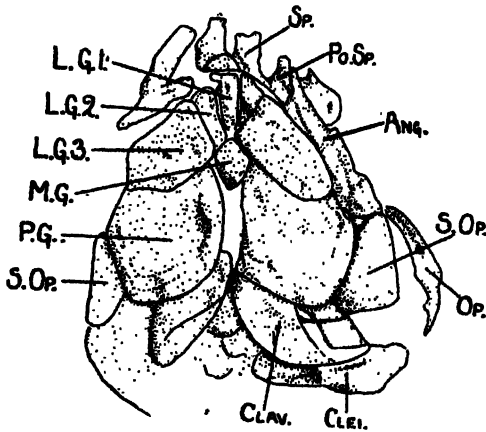
the Groupl in Orkney, combined the two species. Watson and Day pointed out a distinguishing feature in the fusion in *D. platycephalus* of the tabulars and interparietal with the bones immediately in front of them, which remain separate in *D. valenciennesi*.

Amongst the hundreds of specimens of *D. valenciennesi* which we have seen, only three show the bones of the cranial roof clearly; few show anything of the gular apparatus, and only one shows the lateral surface of the head clearly.

Our existing knowledge of the structure of the head still depends in the main on Pander's excellent description and figures. The only addition is Dr. Traquair's well-known restoration.

One specimen (fig. 32), now in D. M. S. Watson's collection, shows the side of the head nearly perfectly. Its structure will be best understood from the figure; the interesting features are the relatively small number (seven) of circumorbitals, the presence of two small elements in the cheek, representing some part of the greatly-developed bones in this region in Osteolepids, and the presence of a very slender, toothless maxilla, lying below the orbit.

FIG. 33.



*Dipterus valenciennesi*, Sedg. & Murch. Ventral surface of head.  $\times 2$ .

From a specimen in D. M. S. Watson's collection.

ANG., angular; CLAV., clavicula; CLER., cleithrum; L.G. 1-3, lateral gulars, nos. 1-3; M.G., median gular; Op., operculum; Po.SP., post-splenial=preangular; P.G., principal gular; S.O.p., sub-operculum; SP., splenial.

There is an indication of an inner ring of circumorbitals, already represented in Dr. Traquair's restoration.

This specimen shows the operculum and a section across the suboperculum, that bone having been driven outward and its upper half thereby removed in the counter slab when crushed down on the rigid clavicular arch. The sub-operculum is followed by a large principal gular, which supports a large lateral gular.

In a triangular space between these two gulars and the articular region of the lower jaw lie three small bones, which can only be lateral gulars. These little bones are also shown in identically the same form in the specimen No. 770, Hugh Miller Collection, Royal Scottish Museum.

The gular apparatus is, however, best seen in the original of fig. 33., a small specimen crushed directly vertically and viewed from the ventral

surface. Here the space between the rami of the lower jaw is mainly occupied by the two pairs of large gular plates already described; but in advance of these are three other small bones, two of which are obviously a pair meeting in the middle line, whilst the other more lateral element which on the right side separates them from the anterior end of the large gular is concealed on the left side by a forward displacement of that bone. At the spot where the four large gulars meet is a small median lozenge-shaped element, already figured, as were the large gulars, by Pander.

No specimens known to us show the structure of the shoulder-girdle completely.

There are a scale-like post-temporal and supra-cleithrum connecting the upper end of the cleithrum with the tabular. The cleithrum is an elongated, narrow bone with a recess on its outer surface for the reception of the hinder edge of the operculum. It is so rigidly attached to the clavicle, that that bone usually retains its natural position and shape in the fossils, having resisted the crushing which disarticulates most of the other bones.

There is some evidence (Peach Coll., No. 35, Royal Scottish Museum) that this attachment is effected by a special downwardly-projecting process on the inner surface of the cleithrum, which is received in a recess in the clavicle: that, in fact, the structure here is exactly as in *Sagenodus*.

The clavicle is a massive bone turning inward and forward onto the ventral surface, and with its fellow filling up the triangular space between the principal gulars.

There is some evidence of a large scale in the position of an interclavicle.

#### DIPTERUS PLATYCEPHALUS, Ag.

We are unable to add much to the existing knowledge of the skull of *D. platycephalus*. No specimen known to us shows the circumorbitals in intelligible form, and none gives an altogether satisfactory view of the opercular region. No. 1059, Hugh Miller Collection, Edinburgh, and Pander's figures, Taf. 3, fig. 17, and Taf. 4, fig. 26, show only three bones on each side—an operculum, sub-operculum, and a gular; no other specimens show additional elements, and it is thus possible that the apparatus was far more reduced than in *D. valenciennesi*, although the material does not admit of definite statements.

The structure of the lower jaw (*cf.* fig. 34, p. 208) is perfectly shown by No. L.10858 of the Manchester Museum. The general features of the morphology were accurately figured by Traquair, but that author was not acquainted with certain very important characters, vividly shown in our specimen.

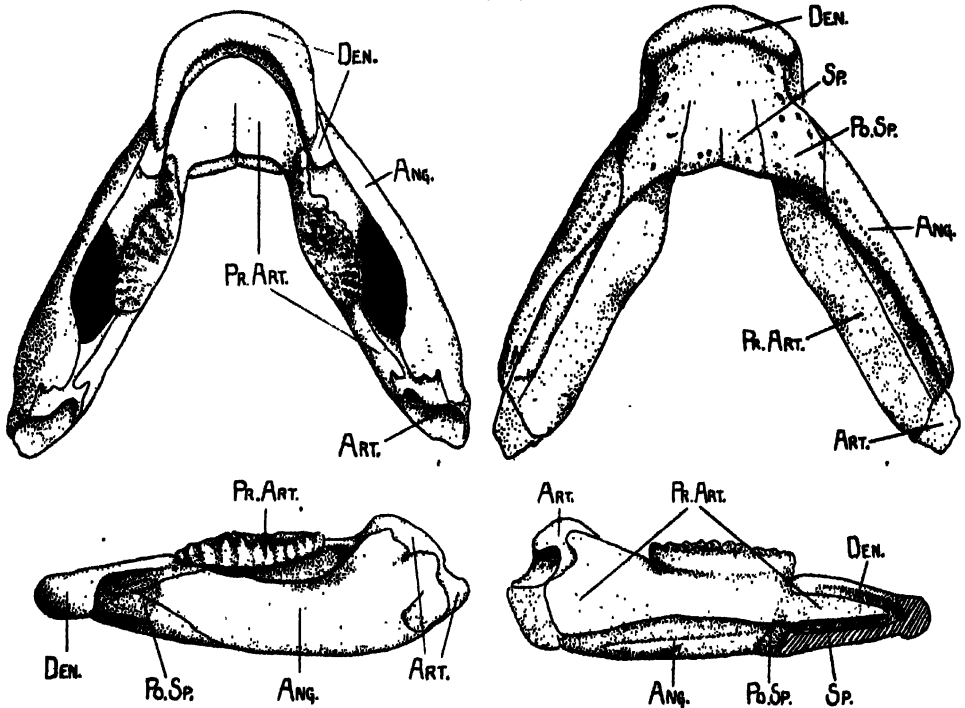
The dentaries are small elements forming a rim to the anterior end of the mandible; the two bones are indistinguishably fused. In section their outer surface forms nearly three quadrants of a circle passing smoothly from the



lower upward into the oral surface; this surface is covered with the shiny punctate surface now recognized as characteristic of a cosmoid bone. This region projects forward, and is sharply marked off from the rest of the lower jaw by depressions on the nearly vertical lateral surfaces.

The dentary articulates with three other bones which lie on the outer surface of the jaw; these are, a very small splenial lying anteriorly on the flat under surface of the chin, a somewhat larger post-splenial which forms part of the floor of the lateral depression, in addition to a large part of the ventral surface, and a very large angular which extends backward to articulate with the articular.

FIG. 84.



*Dipterus platycephalus* (Ag.). Dorsal and ventral views of the lower jaw, with inner and outer aspects of the left ramus.  $\times 1\frac{1}{2}$ . Restored from No. L. 10858, Manchester Museum.

ANG., angular; ART., articular; DEN., dentary; Po.SP., post-splenial = preangular; Pr.ART., pre-articular; SP., splenial.

The presence of splenial, post-splenial, and angular elements is clearly confirmed by No. 1878.5.166, Royal Scottish Museum, where these bones are seen from the dorsal aspect, the tooth-bearing bones being removed.

The articular is a very large bone, with a well-defined condylar surface formed by a deep cylindrical excavation running across its hinder surface

and passing very obliquely backward. The bone is continued forward for a considerable but uncertain distance in contact with the inner surface of the pre-articular.

The pre-articular is the bone usually called splenial in *Ceratodus*. In *Dipterus platycephalus* it is of great length, extending from the articular facet to a symphysis with its fellow, which extends forward nearly to the anterior end of the jaw.

Its hinder part is a vertically placed thin sheet of bone, tightly applied to the inner surface of the articular, with a free upper margin which forms the border of the supra-Meckelian vacuity, and with its lower border in contact with a depressed strip of bone which appears to be a part of the angular, but is perhaps, as Dr. Stensio has suggested to us, really the ossified Meckel's cartilage. It is possible that in the naturally articulated jaw the strip was completely covered by the pre-articular, and that in consequence the ramus is represented as of too great a depth in fig. 34.

From a point not far in front of the articular to the hinder end of the dentary the upper edge of the pre-articular is turned outward and the bone thickened; anteriorly this edge meets the angular, forming the border of the very large supra-Meckelian vacuity.

This out-turned edge of the pre-articular bears the tooth-plate, which is a thick pad with denticulated ridges radiating from a point on the inner border rather behind the middle. The pattern of these teeth-plates differs considerably in individuals; they commonly extend much further forward than in fig. 34.

The pre-articular is completed by turning inward as a flat, nearly horizontal plate to the symphysis, which lies on the dorsal surface of the splenials.

In the reconstructions represented in fig. 34 the ramus may be made too deep and wide. The depth illustrated depends on the actual depth in the specimen; the width is fixed by that of the hinder end of the dentary and of the tooth-bearing part of the pre-articular. At the most, the inaccuracy can only be of the order of one or two millimetres.

The course of the lateral-line canal on the lower jaw is well shown in the specimen. Along the lower border of the angular it is represented by an irregular and often double series of very small pits.

On the post-splenial are two definite lines of large pits, one passing forward parallel to and just within the lower margin of the lateral depression, the other along the hinder border of the bone; in addition, there are other scattered pits. The splenial has two pits near and parallel to its hinder margin.

The new information about *Dipterus* recorded above adds very considerably to the evidence in support of the view first definitely stated by L. Dollo that *Dipterus* is by far the most primitive, as it is the oldest known Dipnoan.

*Dipterus* is now shown to resemble the Osteolepids in the following ways :—

1. In the typical cosmoid structure of its scales.
2. In the general body form, possession of two separate dorsal and an anal fin, and a heterocercal tail with an epichordal lobe.
3. In the number and relations of the dermal bones of the top of the head.
4. In the presence of splenial and post-splenial bones in the lower jaw.
5. In the possession of a very elaborate opercular apparatus, including opercular and sub-opercular, a series of lateral gulars, a pair of principal gulars, and a median gular.
6. In the structure of its paired fins.

These resemblances are of a fundamental character, and imply a community of origin of the two groups.

The principal features in which *Dipterus* differs from an Osteolepid are :—

1. The loss of the hyomandibular as a bone playing a part in the support of the quadrate.
2. The suppression of the suprapterygoid ossicles and the possession of a symphysis between the pterygoids anteriorly, and of a sutural attachment of the pterygoids to the edges of the parasphenoid.
3. The loss of the palatine and ectopterygoids, and the development of a "tooth-plate" on the pterygoid.
4. The loss of the coronoids and the development of the tooth-plate on the pre-articular.
5. The great reduction of the marginal tooth-bearing bones, the pre-maxillæ, maxillæ, and dentaries.
6. The forward inclination of the quadrate, with a correlated shortening of the lower jaw and a great reduction of the cheek-plates.
7. The removal of the external nares from a point on the upper surface to a position below the lip.
8. The absence of a movable joint between the parietals and frontals, and of an unossified region of the basis cranii between the basi-occipital and basisphenoid.

Numbers 1-6 of these differences are obviously dependent on different food habits, the Dipnoi having adopted a diet which required trituration, whilst the Osteolepids are predaceous, swallowing their prey entire.

Difference number 7 may perhaps have arisen not as an adaptation, but as a mere result of the mode of development of the olfactory organ in a fish which has a much reduced maxilla.

The differences recorded under No. 8 can only be explained by supposing these peculiar characters to have been acquired by the Osteolepids after their separation from the Dipnoi.

Thus we are driven to conclude that the Dipnoi, although they have undoubtedly been derived from a stock whose general morphology was Osteolepid, were separated from that stock before its members acquired their most peculiar and diagnostic features.

Comparison of the head of Dipnoi with that of an Osteolepid, the homologies of whose bones are obvious in the light of the structure of Palæozoic amphibia, throws great light on the determination of the elements of the skull.

The very interesting observations recorded by Prof. Goodrich in his general work on Fishes (1909) were the first correctly to lay down the main lines of the comparison between the skulls of Dipnoi and Osteolepids, especially in their recognition of the distribution of the lateral-line canals on the top of the head.

Gregory (1915) further extended this comparison, and finally a comparison of the skull-roof of *D. valenciennesi* with that of the Osteolepids led Watson and Day to an identification of nearly all the bones which compose its apparently inexplicable mosaic.

This interpretation depends on the belief that in *D. platycephalus* the tabulars and post-parietal have fused with the parietals and supratemporals. The lack of a specimen of this species with the skull in articulation with the trunk renders the evidence incomplete, but the fact that the posterior row of three bones in all later Dipnoi houses the occipital cross-commissure of the lateral line shows that it includes these bones; and the well-known pair of grooves on the median occipital, which are for a line of pit organs and are obviously homologous with a similar pair of grooves on the parietals of Osteolepids and some other fish, show that this bone includes the parietals.

In the lower jaw of *Dipterus* the dentary, angular and articular are readily identifiable, and the relations of the splenial and post-splenial to the dentary and angular are so exactly those which obtain in Osteolepids and indeed in Labyrinthodont amphibia as to leave no doubt of their homologies. The only remaining bone, that which bears the tooth-plate, cannot be the splenial, as has been previously believed, because an undoubted splenial occurs in the same jaw. It can only be pre-articular or coronoid: the application of its hinder end to the inner surface of the articular, its large size and position on the inner surface of the ramus, show that it is a pre-articular, and the symphysis which it makes with its fellow can be matched in the case of the pre-articular of *Megalichthys*.

In all Osteolepids and Labyrinthodonts the teeth-bearing bones of the upper and lower jaws have certain quite definite relations to one another. The dentary bites within the maxilla, the teeth on the coronoids interlock with those on the palatine and ectopterygoid, and the upper edge of the pre-articular, which is usually covered with a granulation of small denticles, faces although it does not touch the similarly armed pterygoid. If, as seems to

be clearly the case, the tooth-plate on the pre-articular of *Dipterus* be a development of this customary granulation, then the similar upper jaw structure on which it grinds must have been derived from the similar granulation on the pterygoid. It is improbable that this large tooth-bearing bone on the palate can be a conjoint pterygoid and palatine as is usually believed, because the palatine teeth of Osteolepids are always long tusks, unlikely in any case to be worked up into so typical a crushing structure as the Dipnoan dental plate, and were the palatine preserved, we should expect to find that the lower plate was of coronoid derivation. Nothing in the structure of the *Dipterus* lower jaw supports this view, which can, however, never be disproved because of the possibility (although we think general great improbability) of a fusion of bones.

The opercular apparatus of *D. valenciennesi* is readily interpretable in comparison with that of an Osteolepid. Its unusual feature, the direct contact between the principal gular and the sub-opercular, is probably due to the great reduction of the hinder lateral gulars which is associated with the shortening of the jaw. The meeting of the two rows of lateral gulars in the front is paralleled in *Megalichthys* (No. 28308, Museum of Practical Geology).

The problem of the relationships of the known Dipnoan genera to one another is still incapable of satisfactory solution, because of paucity of material.

The position of *Dipterus valenciennesi*, at the base of the series, seems to be made certain not only by the fact that it is actually the oldest known species, but by the close comparison which can be drawn between its structure and that of an Osteolepid.

From this form the series *D. platycephalus*, *Pentlandia*, *Scaumenacia*, *Phaneropleuron*, first suggested by Prof. Dollo and supported from new evidence by Watson and Day, seem to have arisen. These forms first appear in time in the order named, and show a steady progressive change, resulting in a reduction of the dermal bones in the front of the head, a reduction of the ossifications in the chondrocranium, a loss of the inter-frontal and internasal elements, and a gradual fusion of the median fins with one another. All known features of their structure are consistent with direct descent of any form from that which precedes it.

The new facts about the structure of *Sagenodus* and *Ctenodus* brought forward in this paper show that Watson and Day were not justified in separating them widely from one another and in deriving *Sagenodus* from *Phaneropleuron*.

The descriptions we have given show that the two animals are closely related, that indeed the Lower Carboniferous "*C. interruptus*" is in its teeth in many respects intermediate between the Coal-Measure forms of the two genera. *Ctenodus* has the less reduced skull-roof, which by its retention of

interfrontal and internasal bones demands descent from a form not later than *D. platycephalus*, and cannot have arisen from the much more reduced skulls of *Pentlandia*, *Scaumenacia*, and *Phaneropleuron*.

The *Sagenodus* skull-roof can readily be derived from that of *Ctenodus*. In its dentition *Sagenodus* is much more primitive than *Ctenodus* in retaining the Dipterine arrangement of radiating ridges on the tooth-plates; in fact, *Sagenodus* and *Ctenodus* seem to afford an illustration of the fact, of not uncommon occurrence and great theoretical interest, that if one of two allied closely-related forms is more specialized in a certain region than the other, it will be less advanced in the structure of some other region.

The comparison between the structures of *Sagenodus* and *Ceratodus* included in the description of the former genus seems to us to establish the descent of the latter from the former animal.

The Dipnoi from the Old Red Sandstone probably lived in unusual conditions. J. Barrell has brought forward a mass of evidence to show that, in common with the other fish of the Old Red Sandstone, they were inhabitants of an arid region with seasonal rainfall, living in rivers which were liable to dry up during part of the year and in shallow and impersistent lakes. Although we believe that this view cannot be upheld in its entirety—for it is difficult to conceive of the Caithness flags being deposited anywhere except in a very extensive and permanent sheet of water—it is undoubtedly well founded in its general conclusions.

The Coal-Measure Dipnoi lived under entirely different conditions in pools, often, as in the case of that in which the roof of the Low Main Seam at Newsham was deposited, of very considerable size and permanence. These pools seem to have lain in the midst of the coal-producing forests in a climate which was in no way arid. Thus this difference in habitat at once affords an explanation of the absence of any direct descendant of the *Phaneropleuron* line and the occurrence of a stock not known from the Upper Devonian.

There remain for consideration the remarkable *Uronemus* and *Conchopoma*.

These animals have been associated with one another, though only very doubtfully, by Traquair and Smith Woodward, because of the replacement in them of typical dental plates by isolated small denticles.

Comparison of the figures and description given in this paper will show that there are no valid reasons for believing in the close affinity—that, in fact, they differ so greatly as to be in all probability merely functionally parallel modifications of very different stocks. *Uronemus* has a skull-roof retaining interfrontal and internasal bones, but much reduced by the loss of the bones on the lateral edge of the temporal region behind the squamosal, and of others forming the roof of the skull. *Conchopoma*, with a much more reduced skull-roof, loses the internasal, has a much enlarged interfrontal, exhibits a fusion of the frontal, intertemporal, and post-frontal, and retains

the bone behind the squamosal. So far as the skull-roof is concerned, *Uronemus* might be derived from *Ctenodus*, *Conchopoma* from *Sagenodus*.

In the palate the two genera differ very widely. *Uronemus* has a small parasphenoid, with a long posterior stem and a lozenge-shaped palatal part completely devoid of teeth. The pterygoids form an exceptionally large part of the palate, have a single series of large teeth along their outer margin, and an area covered with small teeth which show no trace of arrangement in radiating ridges. *Conchopoma* has a unique parasphenoid with a long, slender, posterior stem, and an enormously enlarged palatal part extending far forward and covered with an irregular development of small denticles. The pterygoids form narrow slips along the lateral borders of the parasphenoid, bear only a few small teeth, and present no trace of the enlarged marginal teeth of *Uronemus*.

Both forms are unexpectedly primitive in retaining dentaries in the lower jaw, in addition to those splenials which have usually been called by that name in *Ceratodus*.

It now falls to be considered whether all the ancestors of these fish had only isolated denticles, or whether they have arisen separately by the breaking up of dental plates.

Semon showed that in development the dentition of *Ceratodus* begins as a series of isolated denticles supported by a net-work of bony spicules, and that the tooth-plates of the adult are built up by the confluence of such denticles.

This mode of development is consistent with the view that *Uronemus* may have arisen from a form with tooth-plates, because its isolated denticles may merely result from the carrying on to adult life of a structure which occurred in larval stages. It is probable that a stage with distinct unfused denticles formed a larger part of the life-history in early Dipnoi than it does in *Ceratodus*; indeed, the small plate figured by Pander as *D. tuberculatus* (Taf. 5, figs. 20-21) seems actually to consist of individual denticles placed on a bony base.

The whole structure of the Dipnoan skull, the short mouth and forwardly-directed quadrute, the rigid attachment of the pterygoids to the basis cranii, and the reduction of the hyomandibular, all point to the Dipnoan stock being specially modified for the use of a highly-developed crushing dentition. All these changes can be paralleled in those other groups of fishes which have developed analogous tooth-plates.

Thus we believe that a typical tooth-plate like that of *Dipterus* was probably of very early introduction into Dipnoan structure, its production having in fact gone on *pari passu* with the other correlated changes in the head.

We are thus led to believe that *Uronemus* and *Conchopoma* are derived from fish which had tooth-plates, and as no such fish either has or needs a parasphenoid dentition, that the well-developed denticles on that bone in the latter fish are new developments.

## SUMMARY.

This paper includes the first complete accounts of the circumorbital region and opercular apparatus of *Dipterus valenciennesi*, and of the lower jaw of *D. platycephalus*. It gives very nearly complete descriptions of the skull, lower jaw, and clavicular apparatus of *Sagenodus* and *Ctenodus* which much extend our knowledge of these fish. In it the structures of the anterior end of the rare fish *Uronemus* and *Conchopoma* are described and figured for the first time.

*Dipterus* is shown to be directly comparable with Osteolepids in the structure of the opercular apparatus and the lower jaw, in addition to the many previously known resemblances. It is thereby shown that, as its early date would indicate, it is the most primitive known Dipnoan.

*Ctenodus* and *Sagenodus* prove to be closely allied, and a detailed comparison shows so great a similarity between the latter fish and *Ceratodus* as to leave no doubt that it is essentially ancestral to it.

*Uronemus* and *Conchopoma* resemble one another only in the reduction in them of the tooth-plates to isolated denticles. In the structure of the palate and of the roof of the head they differ so much that they must represent widely-separated stocks.

In the main, the trends of Dipnoan development suggested by Watson and Day are confirmed. It is, however, pointed out that the structure of the neural cranium of the Osteolepids, as described by Bryant in *Eusthenopteron*, is such that the Dipnoi cannot be direct descendants of that group, but that with it and the Amphibia they arose together from common ancestors at a time before the Middle Devonian.

We have to thank Dr. A. Smith Woodward, of the British Museum, Dr. Kitchin, of the Museum of Practical Geology, Dr. Tattersall, of the Manchester Museum, and especially Drs. Eagle Clarke and J. Ritchie, of the Royal Scottish Museum, for the use of the materials in their care.

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On the Method of Oviposition and the Egg of *Lyctus brunneus*, Steph. By  
A. M. ALTSON, F.E.S. (Communicated by Dr. A. D. IMMS, F.L.S.)

(PLATE 12 and 2 Text-figures.)

[Read 15th February, 1923.]

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INTRODUCTION.

IN April 1920, the writer commenced an investigation on *Lyctus*—Powder-post—beetles attacking seasoned hardwoods, with a view to devising control measures against their ravages.

This paper is a part of one originally written dealing with all those various aspects of *L. brunneus* which had not been recorded, but owing to the cost of getting the whole published, it has been found necessary to cut it up into sections, and this constitutes the first part.

There are two species of beetles of the genus *Lyctus*, family Lyctidae, so far recorded in the British Isles. They are *Lyctus* (*Xylotrogus*) *brunneus*, Steph., and *Lyctus linearis*, Goeze (*canaliculatus*, Fab., *oblongus*, Oliv., *striatus*, Melsh., *unipunctatus*, Herbst). Both species breed in dry or seasoned hardwoods, usually attacking the sapwood only, although *L. brunneus* was found attacking the sap- and heartwood of mahogany (*Ahaya* sp.), and Noerdlinger (1862) recorded *L. linearis* as attacking sap- and heartwood of black locust (*Gleditschia triacanthos*).

In 1891 Fowler recorded *L. brunneus* as very rare, and *L. linearis* (*canaliculatus*) as common; the contrary is now the case. Hopkins (1911) considers *brunneus*—now widely distributed throughout the world—to be of S. American origin, and *linearis* of European origin.

REVIEW OF THE LITERATURE.

Amongst the mass of literature on Powder-post beetles, there has been very little published upon *L. brunneus*, and what there is deals mainly with its

ravages, but on the other *Lyctus* beetles there are some descriptions of oviposition, and in three cases an egg is described.

In 1853 Heeger figured and described an egg, a legless larva, and a pupa, which he ascribed to *L. pubescens*, Panz.

In 1855 Noerdlinger described the larva, pupa, and adult of *L. linearis* (*canaliculatus*), and in an account of the habits stated that the eggs were deposited in cracks or fissures.

In 1874 Kaltenbach refers to the habits of the larva of *linearis* (*canaliculatus*) and to that of *pubescens*, quoting Heeger as his authority in the case of the latter.

In 1876 Perris described and figured the larva of *linearis* (*canaliculatus*), and disputed the accuracy of Heeger's description of a legless larva of *pubescens*.

In 1880 Kittel described—after Noerdlinger (1855)—the larva, pupa, and adult of *linearis* (*canaliculatus*).

In 1883 Dugès described and figured the larva, pupa, and adult of *L. planicollis*, Le Conte (*L. carbonarius*, Waltl.), to prove that the legless larva described and figured by Heeger could not belong to the genus *Lyctus*.

In 1890 Rye refers to the discovery of a legless larva of "a species of *Lyctus*" (?).

In 1898 Xamheu described the life-history of *linearis* (*canaliculatus*) including a description of the egg, and stated that the eggs were deposited in cracks or fissures; this description was corroborated by Bureau (1900), and since by several writers.

In 1916 Snyder described the egg and manner of oviposition of *planicollis*, and figured the egg. This egg differs from that of *pubescens* as described and figured by Heeger, and from that of *linearis* as described by Xamheu, but it is practically identical in appearance with the egg of *brunneus* found by the writer. This similarity between the eggs of *planicollis* and *brunneus* is maintained up to the time of maturation of the larva (Pl. 12. fig. 4), but the method of the larva's hatching differs.

Oviposition in *brunneus* is similar to that of *planicollis*, and it is not as described by French in 1918, who states:—"The female (*brunneus*) deposits her eggs on the outside, underside, and ends of the timber." The eggs are deposited inside the timber.

#### MATERIAL USED.

Most of the infested material from which *L. brunneus* was bred was obtained in London from hardwoods stored in a timber yard, where the presence of the beetle had been known for a few years.

Pieces of infested wood were collected in April 1920. The beetle was then still in the larval stage. In May of the same year, a small quantity of the infested material was placed in a refrigerator with a constant temperature

of 8° C. to retard development; this material was withdrawn in July 1920 and enabled the writer to verify the observations on oviposition and the egg at leisure.

The infested woods collected were West African mahogany (*Khaya* sp.), "Wainscot" oak (*Quercus Robur*), and "Italian" walnut (*Juglans regia*). Beetles were also bred from locust (*Robinia pseudacacia*).

Unfortunately no living specimens of *L. linearis* were obtained, although efforts were made in various directions to procure some. No beetles emerged from two pieces of oak—hitherto infested with *L. linearis*—which were sent over from Paris, nor were any living larvæ or pupæ found. Dr. C. J. Gahan informed the writer, that no record of the capture of this beetle in the British Isles had come to his notice for some years.

#### MATING.

The beetles are sexually mature when they emerge. Mating takes place immediately after emergence either at dusk or during the night. It was observed in daytime; and on several occasions two beetles were found occupying the same pupal chamber, but in no instance was mating observed to last very long. Individual males fertilize several females, therein differing from *L. linearis* as described by Xambou (1898), who stated coition lasted the entire night and the male then dies. In *brunneus*, females considerably outnumber the males.

The length of the life of the females when free to mate and oviposit averaged about six weeks; the males lived two to three weeks. The food of the adults consists of particles of wood-tissue.

#### OVIPOSITION.

The ovipositor is an exceedingly long and flexible organ, and when fully extruded (Pl. 12. fig. 1) it is nearly the length of the beetle.

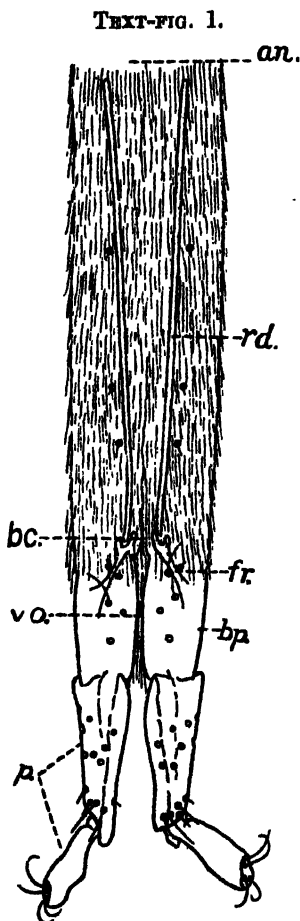
Oviposition begins two to three days after mating and takes place, at dusk or during the night, in the tracheæ, or vessels, or pores of the wood. Consequently those woods in which the vessels are most numerous are most liable to heavy attacks.

The female either projects the ovipositor directly into the vessel, or it is curved down and bent forward in the vessel underneath the body. Before actually inserting the ovipositor into a vessel, a preliminary examination of the surface is made with the ventral pygidial palps, and after selecting a vessel the ovipositor is slowly inserted, and apparently a further examination is made within the vessel by the vaginal palps (*p*, text-fig. 1) on the apex of the ovipositor; when, if the conditions are suitable, two or more eggs are deposited. The number, however, depends upon the suitability and capacity of the vessel. For, when an obstruction is encountered—in the form of broken down transverse walls, etc.—only one or two may be deposited, or the ovipositor will be withdrawn and another vessel tried.

The eggs are always laid longitudinally in the vessel and in juxtaposition, the anterior pole of one being end on to the posterior pole of the next.

A female will retain the ovipositor in the vessel for several minutes, and repeat the process in other vessels until her supply of ripe eggs is exhausted.

The egg issues from the vaginal orifice (*vo.*, text-fig. 1) between the basal pieces (*bp.*), and is guided by the vaginal palps (*p.*).



Apex of the ovipositor, ventral. *an.*, anus; *bc.*, bursa copulatrix; *bp.*, basal piece; *fr.*, forked rod; *p.*, vaginal palp; *rd.*, chitinised rod; *vo.*, vaginal orifice. *Camera lucida.* ( $\times 128$ .)

From observations on a beetle when ovipositing, it was noticed that she moved forward once before withdrawing the ovipositor; apparently the movement was just far enough to allow for a space for the second egg to be deposited in

Oviposition also takes place—in the case of previously infested wood—in those vessels which have been bitten across in the pupal chamber and its extension to the exit-hole.

It was observed that, when the beetles are feeding on the surface of the wood, they always bite the tissues transversely; this habit—if the wood is longitudinally split—not infrequently cuts open a vessel and creates a point of access to it. In several instances, examination has shown that this opening in the vessel has been used for the deposition of eggs.

The eggs are deposited in the vessels at varying distances from the point of access of the ovipositor, but the anterior pole of the last egg laid is seldom less than 1 mm. from it. In one specific instance in which three eggs were found, the distance from the point of access to the posterior pole of the first egg deposited was 3.75 mm.; on two occasions five eggs in juxtaposition were found, in these cases the ovipositor had been inserted more than 5 mm.

The eggs were difficult to find and very easily broken when shaving off the wood-tissues in search of them, and when exposed, the task of removing them or “digging” them out is an exceedingly difficult one. The writer estimates that on an average 75 per cent. of the eggs were lost in trying to locate them, and probably 60 per cent. of the located eggs were damaged or destroyed in endeavouring to extract them from the vessels.

From the examination of several ovaries, it was found that in the case of fertilized females, only a small number of eggs mature at a time, eight to twelve being the usual number found collected in the calices. In the case of unfertilized females, the ripe eggs continue to pass into the calices until the latter become swollen and the death of the female ensues.

### THE EGG.

Pl. 12. fig. 2 is a photograph of deposited eggs *in situ*; part of the vessel and surrounding tissues have been removed.

The egg is translucent white and cylindrical; tapering towards and rounded at the posterior pole. The anterior pole is rounded, but continuing from it, as if broadly attached to it, is a long, slender tube-like process which terminates in a round protuberance.

This process varies considerably in length even in those eggs laid by one female. The process was never observed to be attached to the walls of the vessel, but when two or more eggs had been deposited in the same vessel it was usually found adhering to the egg next to it.

The chorion is creased longitudinally, giving the egg the appearance of being marked with longitudinal striæ, which concentrating at the anterior pole are more pronounced in this area. These striations and the process or strand were found to owe their origin to the action of chitinised setæ lining a pair of valves situated at the junction of the oviducts, and are the result of the pressure exerted by the valve upon the egg as it is forced through on its passage.

A ripe egg removed from the calices of a female does not show the process or striations, and would thus agree with Xamheu's (1898) description of the egg of *L. linearis*.

The recently deposited egg (Pl. 12. fig. 3) has a distinct granular appearance, due to the exceptionally large yolk granules.

The size of the deposited eggs was found to range from 1.25 mm. to 0.8 mm. in length without the process, which varied in length from 0.2 mm. to 0.35 mm., and the width of the egg ranged from 0.15 mm. to 0.175 mm. During maturation the egg slightly increases in size.

In eight specific instances, comprising 13 eggs under observation, the young larva reached maturity 15 days after the egg was laid. That is, movements of the larva were visible within the chorion at that period. The actual number of hours any of these eggs took to reach this stage is not known, as the time at which oviposition took place was not observed. But the small pieces of wood in which the beetles were allowed to oviposit were put in their cages—glass-topped tins—in the evening and collected the following morning, 12 to 16 hours later.

At the time of maturation or when the first movements of the larva are visible, it occupies approximately half the length of the egg (Pl. 12. fig. 4) and is situated in the posterior portion; the anterior portion, from the base of the process to the head of the larva, is occupied by a mass which consists of large yolk granules and fat bodies. The writer has observed that this extraordinary mass\* constitutes in *L. brunneus* the initial food of the young larva whilst still enclosed within the chorion.

In the case of *L. planicollis* it is stated that: "In hatching, the larva backs out of the egg" (Snyder, 1916). It is the reverse with *L. brunneus*. So soon as the larva is matured, it commences to eat the residual yolk-mass situated in the anterior portion of the egg by means of its mandibles, and travels forward to do so. If an egg is completely exposed in the vessel, the larva is unable to consume the entire residual yolk-mass, owing to its movements and the lack of "overhead" support—the wall of the vessel—it usually breaks the chorion and works its way out of the vessel. But if small strips of tissue, such as parts of a medullary ray, are left above part of the egg, the larva is able to maintain its position and consume its food, and at the same time the observer is enabled to follow its normal movements.

An examination of longitudinal and transverse sections of a small number of eggs in different stages of development, suggest that the phenomenon of the residual yolk-mass is due to the blastoderm enveloping only a part of the yolk. It was thought that it might be a case of polyembryony, with one or more embryos abortive, but there was no evidence found to support this.

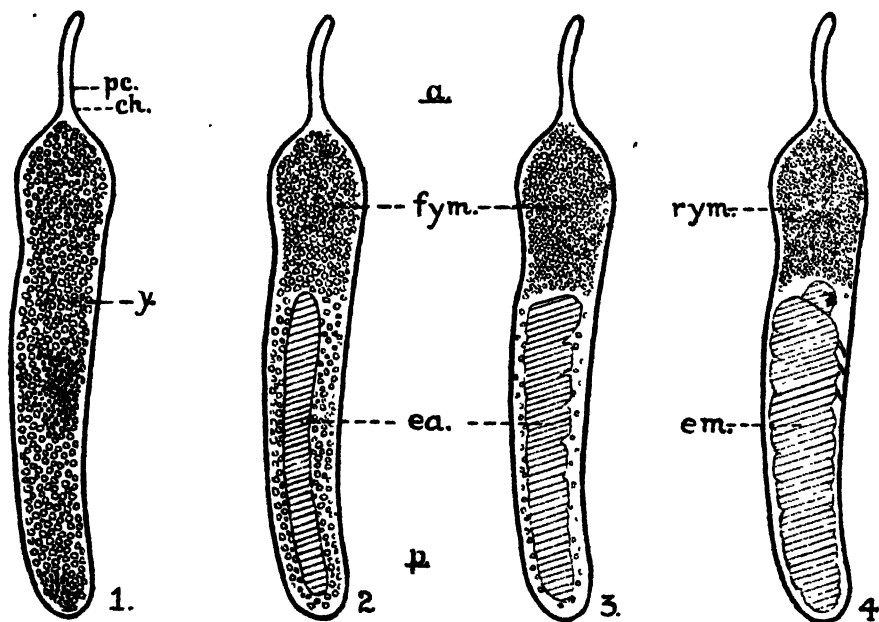
\* Owing to the lack of an existing term for this "yolk-mass"—no analogous yolk-mass being known—the term residual yolk-mass has been suggested and is used in this paper to denote it.

Text-fig. 2 gives a series of diagrammatic sketches showing the maturation of the egg in four stages.

The movements of the larva are easily discernible within the intact covering of the chorion, and it is not until the larva has been feeding for some time that the chorion becomes broken by its movements at the posterior end and later injured in the process of the consumption of its initial food.

Pl. 12. fig. 4 depicts an egg in which the larva has commenced feeding on the residual yolk-mass in which its head is partially buried. (The bend in the egg was due to the movement of the larva when dropped into Carnoy II.) The photo shows that the chorion at the posterior end is broken, and that it is crumpled in the part occupied by the larva, whereas it is quite taut around the anterior part.

TEXT-FIG. 2.



Development of the egg (diagrammatic). 1. Egg twelve hours old. 2. Several days later. 3. About ten days old. 4. Mature egg.

*a.*, anterior pole; *ch.*, chorion; *ea.*, embryonic area; *em.*, embryo; *fym.*, formation of residual yolk-mass; *p.*, posterior pole; *pc.*, process or strand; *rym.*, residual yolk-mass; *y.*, yolk.

#### LOCATING THE EGGS.

In the first instance the beetles were caged in a cavity ( $1\frac{1}{2}$  inches in diameter) cut with a brace and bit in pieces of mahogany (4 inches by 3 inches by 1 inch thick). The cavity, which was full of cracks, fissures, and crevices, was about  $\frac{1}{2}$  inch deep, and it and the surface of the piece of wood were covered with a piece of glass held in position with elastic bands.

Shaving off the wood with a scalpel under binoculars in search of the



eggs, after the manner of oviposition was established, proved far from satisfactory and extremely laborious owing to the mass of wood which had to be cut away from the sides to shave down those parts to get near the vessels which had been opened transversely and accessible to the beetles. And so another and entirely successful method was adopted.

Glass-topped tins were used as cages. Into these small pieces of mahogany were put for the beetles to oviposit in. The sizes of these pieces, which were split on all faces longitudinally with the vessels, and cut transversely at the ends, ranged from 1 to 2 inches in length by one-eighth to about three-eighths of an inch in width and thickness.

The search for the eggs in these pieces was carried out as above and was mainly confined to the extremities, unless a vessel had been fractured in splitting or bitten open by a beetle.

No attempt was made to find eggs in planks or in the "field."

#### NOTE ON *LYCTUS LINEARIS*, GOEZE.

As no living specimens of *L. linearis* were obtained, the writer's intention, to study the early stages of this insect with a view to critically examining the descriptions of the manner of oviposition and the egg as published by Noerdlinger (1855) and Xamheu (1898), did not materialise.

Several writers since 1898 to 1920 have published corroborative accounts of Xamheu's description of the egg and manner of oviposition. But it has recently been found that in 1917 Hopkins and Snyder—after the latter's discovery of the egg and manner of oviposition of *L. planicollis*—published a paper in which they described the life-histories of *L. linearis*, *L. parallelopipedus*, Melsh., *L. cavicollis*, Lec., and *L. planicollis*, as being identical except as to the time of the emergence of the adults. The inference to be drawn is that the egg and manner of oviposition is similar in these four species and consequently similar to the egg and manner of oviposition of *L. brunneus* as described in this paper.

Therefore Xamheu's description of a strandless egg deposited in cracks, fissures, or crevices can no longer stand.

It will probably be found that this method and manner of oviposition—depositing the eggs in the tracheæ, vessels, or pores—is a generic characteristic of the wood-infesting *Lyctus* beetles.

#### CONCLUSIONS.

The phenomenon of the egg of *L. brunneus* is, so far as it has been possible to ascertain, unlike any case of embryological development recorded, not only in the records of Entomology, but in those of Zoology as a whole ; a case in which within the egg is produced the young larva's initial food.

The closest analogy found is that of a case of polyembryony discussed by Gatenby (1919) in a review on the early development of the egg and the

formation and maturation of the larvæ of a polyembryonic *Encyrtid* (Parasitic Hymenoptera), in which he refers to the existence of abortive embryos. He states: "It is remarkable to find that in the polyembryonic Hymenoptera a large region of the egg is entirely discarded. In fact, just that region of the egg which would have formed the head, brain, etc., of the embryo is rejected."

It is the same area in the egg of *L. brunneus* which becomes the larva's initial food.

The similarity of the egg of *L. brunneus* to that of *L. planicollis*—as described and figured by Snyder (1916)—in their appearance up to the time of maturation, suggests that the embryological phenomenon of the former species must also exist in the latter.

#### SUMMARY.

1. The method and manner of oviposition in *L. brunneus* is established and is found to be the same as in *L. planicollis*, which is that of depositing its eggs in the tracheæ, vessels, or pores, and under the surface of the wood.

2. The eggs incubate in 15 days. The young larva, which occupies barely half the length of the egg, does not hatch out at once, but proceeds to eat the residual yolk-mass contained in the anterior part of the egg.

#### ACKNOWLEDGMENTS.

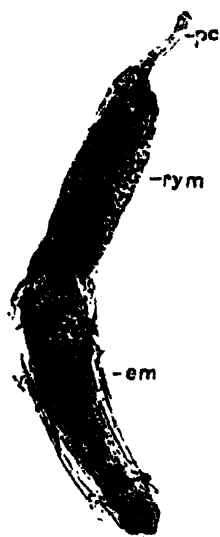
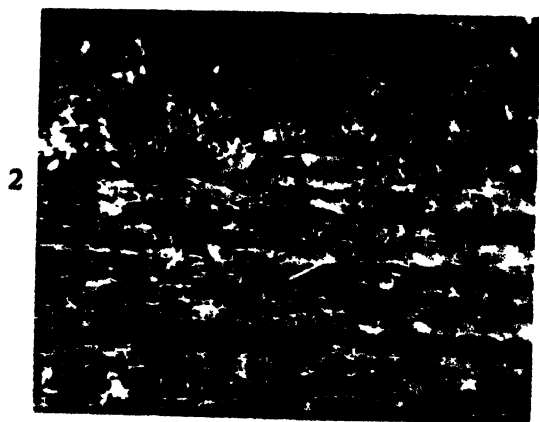
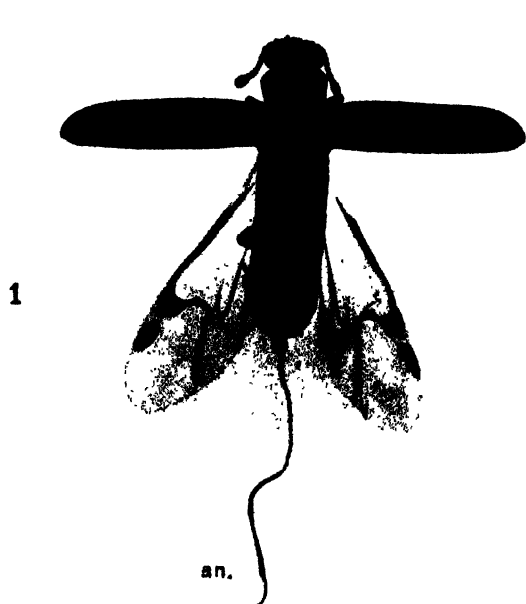
The investigation, of which this paper records part of the results, was suggested by Prof. H. Maxwell Lefroy, Imperial College of Science, to whom the writer has to express his thanks, and to the Committee of the Scientific and Industrial Research Department, for a grant to carry on the work.

The writer is also indebted to Dr. C. J. Gahan, Keeper of the Department of Entomology, Natural History Museum, for identifying specimens of *L. brunneus*; to Prof. Percy Groom, Imperial College of Science, for identifying the various species of timber used in this work; to Dr. L. T. Hogben, lately Lecturer in Zoology, Imperial College of Science, for his advice and assistance in regard to the egg of *L. brunneus*; to Dr. Hugh Scott, Cambridge Museum, for specimens of *L. linearis*; to M. P. Lesne, Muséum d'Histoire Naturelle, Paris, for sending two pieces of oak infested by *L. linearis*; to Dr. J. W. Munro, Forest Entomologist, Board of Agriculture, and to Mr. W. Dallimore, Royal Botanic Gardens, Kew, for material.

In addition, thanks are due to Dr. A. D. Imms, Rothamsted Experimental Station, for his advice and assistance in connection with the publication of this paper; and to Prof. S. MacDougall for his efforts to get the original paper published as a whole.

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A.M.A. Phot

Westwood  
Bequest

LYCTUS BRUNNEUS Steph



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## EXPLANATION OF PLATE 12.

- Fig. 1. Photomicrograph of female *L. brunneus*, with ovipositor fully extended; magnified 7 diameters.
2. Two eggs *in situ* in a piece of mahogany.
3. Photomicrograph of an egg, 12–16 hours old.
4. Photomicrograph of a mature egg.

(Fig. 1 by C. GUNNS; figs. 2–4 by A. M. A.)



Some Echinoderms from West Australia. By HUBERT LYMAN CLARK,  
Museum of Comparative Zoology, Cambridge, Mass., U.S.A. (Com-  
municated by Prof. W. J. DAKIN, F.L.S.)

[Percy Sladen Trust Expedition to the Abrolhos Islands under the  
leadership of Prof. W. J. DAKIN.]

(PLATE 13.)

[Read 1st February, 1923.]

THE collection of echinoderms placed in my hands by Professor Dakin\* prove to be of great interest even though the number of species represented is small. The specimens were taken off the coast of West Australia, chiefly among Houtman's Abrolhos Islands, but a considerable number were dredged near Fremantle, while one interesting specimen comes from Broome. Many of the species are represented by but one or two specimens, and on this account it is not possible to determine the relative abundance of the different forms.

The 143 specimens represent 46 species, of which two (*Ophiactis savignyi*, *Echinocardium cordatum*) are practically cosmopolitan. Of the others, 27 are tropical species, most of which are common in the East Indies; their occurrence at the Abrolhos is notable because those islands are so far south of the usual range of the species; few, if any, extend their range nearly so far southward on the eastern side of the continent.

There are, in the present collection, 8 species which occur on the southern or south-eastern coasts of Australia between Sydney and Perth, though most of them are known from only a few widely separated stations. These, which may be called the typical Australian species, are:—

*Astropecten preissii* Müller & Troschel.

*Luidia maculata australasica* Döderlein.

*Asterina gunnii* Gray.

*Coscinasterias calamaria* (Gray).

*Ophiothrix spongicola* Stimpson.

*Amblypneustes pallidus* (Lamarck).

*Heliocidaris erythrogramma* (Valenciennes).

*Breynia australasica* (Leach).

\* I beg to express here my sincere thanks to Professor Dakin for the opportunity of studying this valuable collection. I would also thank my friend Mr. Austin H. Clark for very important assistance in connection with bibliographical data, which were not available to me.



There are 9 species which seem to be endemic ; at least they are not yet known from anywhere but the coast of West Australia :—

- Pentagonaster stibarus* H. L. Clark.
- Anthenea australiæ* Döderlein.
- Anthenea globigera* Döderlein.
- Nectria macrobrachia*, sp. nov.
- Petricia obesa*, sp. nov.
- Parasterina crassa* (Gray).
- Uniophora dyscrita*, sp. nov.
- Ophiothrix michaelseni* Koehler.
- Centrostephanus tenuispinus* H. L. Clark.

The following species were taken only off Fremantle :—

- Luidia maculata australasiæ* Döderlein.
- Astropecten preissii* Müller & Troschel.
- Asterina gunnii* Gray.
- Parasterina crassa* (Gray).
- Ophiothrix michaelsoni* Koehler.
- Echinocardium cordatum* (Pennant).

Three species were found both at Fremantle and at the Abrolhos :—

- Anthenea australiæ* Döderlein.
- Ophiothrix spongicola* Stimpson.
- Ophiothrix stelligera* Lyman.

From Broome alone, comes a specimen of

- Euryale aspera* Lamarck.

Although Gray described several sea-stars from "Swan River" and "Western Australia" as far back as 1840 (Ann. Mag. Nat. Hist. vol. vi. Dec. 1840, p. 281) and 1847 (Proc. Zool. Soc. London, pp. 75-83), almost nothing else was published dealing with the echinoderms of that region until after the close of the nineteenth century. In 1907, Koehler reported on the collection of ophiurans made by Michaelsen and Hartmeyer between Cape Naturaliste and Sharks Bay in 1905. (See their 'Die Fauna Südwest-Australiens,' Bd. i. Lief. 4.) There were 28 species in this collection, of which only three were new, and most of the others were well-known Indo-Pacific species. In 1911, A. H. Clark published his invaluable report on the "Recent Crinoids of Australia" (Mem. Austral. Mus. vol. iv. pp. 703-804) and also a report on the collections made by Michaelsen and Hartmeyer (Fauna Südwest-Australiens, Bd. iii. Lief. 13), the two papers giving a complete list of Western Australian Crinoids. In 1914, Döderlein reported on the echini brought back by Michaelsen and Hartmeyer (Fauna Südwest-

Austral. Bd. iv. Lief. 12), which included 16 species of which three were new. The same year, Mr. B. Alexander published (1914, Rec. West Aust. Mus. vol. i. pt. iii. pp. 108-112) a list of the echinoderms of Western Australia found in the Western Australian Museum at Perth. This list was based on papers by A. H. Clark and myself published in the same part of the "Records," dealing with the crinoids and the other echinoderms respectively. In his list Alexander records 86 species, of which half a dozen are holothurians. As there are no holothurians in the collection sent me by Professor Dakin I shall ignore that class, and the present remarks deal only with the actinogonidiata echinoderms\*. Alexander includes only ten of the 28 ophiurans of Koehler's 1907 list and only five or six of Döderlein's list of echini, there being some question about certain identifications in this group.

In 1918, Mortensen (Kungl. Svenska Vet.-Akad. Handl., Bd. 58. no. 9) published a report on echini collected by Mjöberg at Cape Jaubert and Broome, a region from which almost nothing was previously known. This collection contained 14 species, of which only four are found in Döderlein's list from the south-western coast. In 1919 appeared Gislén's (Kungl. Svenska Vet.-Akad. Handl., Bd. 59. no. 4) admirable report on the crinoids collected by Mjöberg, in which is given a careful and very valuable account of seven species, one of which had not previously been reported from Western Australia.

Up to the present time therefore, 125 species of echinoderms, not including holothurians, have been reliably reported from Western Australia, and there are perhaps 10 or 11 species which could be added to this list on the strength of old records which may not properly be ignored. This gives us a total of at least 135 species occurring in the region, already reported, but as the Dakin collection contains no fewer than a dozen species not hitherto recorded, it is evident that the total number of echinoderms occurring on the western side of the Australian continent certainly exceeds 150, and it is probably in excess of 200.

It is interesting to examine separately the list of species occurring at the Abrolhos, as those islands are said to contain the southernmost coral reefs in the world. Including the species here recorded, the list of forms known from the Abrolhos is as follows:—

#### CRINOIDS:—

*Cumatella nigra* (P. H. Carp.).  
*C. stelligera* (P. H. Carp.).  
*Cumatula solaris* (Lam.).  
*C. pectinata* (L.).  
*Comanthus annulata* (Bell).

*Comanthus parvicirra* (J. Müll.).  
*C. polyenemis* A. H. Clark.  
*Amphimetra jacquinoti* (J. Müll.).  
*Lamprometra gyges* (Bell).  
*Oligometra serripinna* (P. H. Carp.).

\* [The Holothurians from West Australia are in the hands of Dr. Jos. Pearson, Colombo Museum.—W. J. D.]

## ASTEROIDS :—

*Nectria macrobrachia*, sp. nov.  
*Pentagonaster stibarus* H. L. Clark.  
*Stellaster inaei* Gray.  
*Anthea australis* Död.  
*Anthea globigera* Död.

*Fromia andamanensis* Koeh.  
*F. elegans* H. L. Clark.  
*Bunaster lithodes* Fisher.  
*Petricia obesa*, sp. nov.  
*Asterina burtonii* Gray.

## OPHIUROIDS :—

*Ophiactis saviynyi* (M. & T.).  
*Ophiothrix longipeda* (Lam.).  
*O. michaelsoni* Koeh.  
*O. spongicola* Stimpson.

*Ophiothrix stelligera* Lym.  
*Ophiomercis porrecta* Lym.  
*Ophiocoma brevipes* Peters.  
*Ophioplocus imbricatus* (M. & T.).

## ECHINOIDS :—

*Prionocidaris baculosa* var. *annulifera*  
 (Lam.).  
*P. bispinosa* var. *chinensis* (Död.).  
*Centrechinus saviynyi* (Mich.).  
*C. setosus* (Leske).  
*Centrostephanus tenuispinus* H. L. Clark.  
*Amblypneustes pallidus* (Lam.).

*Salmacis virgulata* Ag. & Des.  
*Pseudoboletia indiana* (Mich.).  
*Tripneustes gratilla* (L.).  
*Helicoidaris erythrogrumma* (Val.).  
*Echinometra mathaei* Bl.  
*Breynia australasiae* (Leach).

Of these 40 species, now known from the Abrolhos Islands, three-fourths may be reckoned as tropical species, for 1 is tropicopolitan, 25 occur in the East Indies, and 4 others occur along the coast of northern or at least north-eastern Australia. Of the remaining 10, 7 are endemic and 3 are South Australian forms. Of the endemic species, 3 (*Nectria macrobrachia*, *Petricia obesa*, and *Centrostephanus tenuispinus*) are most nearly allied to species from the southern coasts of Australia. It is evident, therefore, that the Abrolhos have received their echinoderm fauna chiefly from the north, and that only a very small number of characteristically Australian forms have as yet found a footing among those islands.

## CRINOIDEA.

## COMATELLA NIGRA.

*Actinometra nigra* P. H. Carpenter, 1888, 'Challenger' Comat. p. 304.

*Comatella nigra* A. H. Clark, 1908; *Smithson. Misc. Coll.* lii. p. 207.

A single well-marked specimen dredged off Long Island, Abrolhos. It is nearly black, has 40 arms about 110 mm. long, and the very powerful cirri are XXII, 25-28. The disk is about 32 mm. across, orally. This species has not been recorded hitherto from western Australia, though it is known from the Aru Islands and I found it at the Murray Islands in 1913.

## COMATELLA STELLIGERA.

*Actinometra stelligera* P. H. Carpenter, 1888, 'Challenger' Comat. p. 308.

*Comatella stelligera* A. H. Clark, 1908; *Smithson. Misc. Coll.* lii. p. 207.

A single specimen of this northern species was taken on the shores of Wooded Isle. It is bright yellow-brown, in its preserved condition, is

25 mm. across the disk, and has 25 arms: 90 mm. long more or less. Cirri XXX, 19-22. There is only one record of *C. stelligera* from a point anywhere nearly so far south as Wooded Isle, and that is the isolated and dubious record from Port Jackson. The species ranges from Ceylon to Samoa and is very common at the Murray Islands, east of Torres Strait, but is not known from the coast of Queensland.

#### COMATULA SOLARIS.

Lamarck, 1816, Anim. s. Vert. ii. p. 533.

A specimen with the 10 arms, 125 mm.  $\pm$  long and about 7 mm. wide, near base, was taken at East Wallaby Island. It is almost black, but has a longitudinal light stripe on the dorsal side of each of the arms, which are remarkably stout. A second specimen not quite so large, taken in the dredge off Long Island, has no trace of the light stripe on the dorsal side of the arms. It has the cirri XIII, 18.

#### COMATULA PECTINATA.

*Asterias pectinata* Linné, 1758, Syst. Nat. ed. x. p. 663.

*Comatula pectinata* A. H. Clark, 1908, Proc. U.S. Nat. Mus. xxxiii. p. 685.

This comatulid seems to be rather common at the Abrolhos, as there are 13 specimens in the present collection: 9 dredged off Long Island and 4 dredged near First Island. All are brown, pale brown, or yellow-brown in colour. They are small, only two or three having arms 100 mm. long. The cirri range from I-XIV, with segments 10-14, but in no case are they arranged in pairs at the corners of the centrodorsal as they are in *C. purpurea*. Otherwise these specimens would, because of their small size, be more naturally assigned to that species, which Mr. A. H. Clark has recorded from "between Fremantle and Geraldton." Several of the specimens examined by Mr. Clark were not typical *C. purpurea*, and intergrade evidently with *C. pectinata*. Gislén (1919) has found so much intergradation between *C. pectinata* and *C. purpurea* that he retains the latter name as varietal only, and I am inclined to agree with him that it is certainly not specific. Just what the relation between *C. purpurea* and *C. pectinata* really is requires still further study.

#### COMANTHUS ANNULATA.

*Actinometra annulata* Bell, 1882, Proc. Zool. Soc. London, p. 535.

*Comanthus (Tania) annulata* A. H. Clark, 1911, Mem. Austral. Mus. iv. p. 757.

The seven specimens of this handsome species were all taken on the shores of Wooded Isle. The number of arms ranges from 36 to 47 and their length from 100 to 125 mm.; in the specimen with 36 arms every Br series is 4 (3 + 4), but in the one with 47 there are four II Br series, 2 and one IV Br series, 2. Cirri very weak, V-VIII, 12. The uniformity of these specimens in coloration is their most notable feature, and in this they agree

with seven of the specimens A. H. Clark (1914, Rec. W. Austral. Mus. i. p. 120) records from between Fremantle and Geraldton, except that they apparently have a darker ground-colour. But they are all spotted with uniformly small, circular greenish-yellow dots, generally quite distinct, but obscured in some of the darkest specimens. In view of the extraordinary diversity of colour of this comatulid, at the Murray Islands, it is remarkable that no diversity at all is shown at the Abrolhos. Possibly this western form may be worthy of a varietal name, but further field observations are necessary before a decision can be reached.

#### COMANTHUS PARVICIRRA.

*Alecto parvicirra* J. Müller, 1841, Arch. f. Naturg. vii. p. 145.

*Comanthus parvicirra* A. H. Clark, 1908, Smithsonian Misc. Coll. lii. p. 203.

There are seven comatulids from Wooded Isle which seem to represent this species, though the colour is the yellow-brown characteristic of *C. luteofusca*. They range in size from those with arms 35-40 mm. long up to those whose arms exceed 100 mm. The disk is 7-12 mm. across. The arms range from 12 to 23 in number. The cirri are few and weak, and have the characteristic form and proportions.

#### AMPHIMETRA JACQUINOTI.

*Comatula jacquinoti* J. Müller, 1846, Monatsb. d. k. preuss. Akad. Wiss. p. 178.

*Amphimetra jacquinoti* A. H. Clark, 1914, Rec. W. Austral. Mus. i. p. 124.

There are five specimens of this fine comatulid, but all are more or less badly broken; two were "dredged outside Wallaby Group," while the other three were "dredged off Long Island." They are each about 12 mm. across the disk, and the arms were apparently about 100 mm. long. The cirri are XXI-XXVI, 26-32, 33-39, 36-41, with the segments *all* much wider than long and the dorsal teeth beginning at the 12th-15th segment. The calyx and arms in each specimen are a dirty cream-colour, while the cirri are of that shade only at the base, becoming purple distally.

#### LAMPROMETRA GYGES.

*Antedon gyges* Bell, 1884, 'Alert' Rep. p. 160.

*Lamprometra gyges* A. H. Clark, 1913, Proc. Biol. Soc. Wash. xxvi. p. 144.

There are two light-brown specimens of this species collected along the shore at Wooded Isle. The arms are about 100 mm. long, and their segments proximally are so closely opposed to each other that the basal part of the arm is noticeably smooth and regular. The cirri are XXX-XXXII, 25-30; one specimen shows twenty-three additional cirrus-sockets. The cirri are less brown, more grey than the calyx. In one specimen there can be distinguished along the dorsal side of each fully-developed arm an inconspicuous longitudinal whitish line.

**OLIGOMETRA SERRIPINNA.**

*Antedon serripinna* P. H. Carpenter, 1881, Notes from the Leyden Museum, vol. iii. pp. 175, 182.

*Oligometra serripinna* A. H. Clark, 1908, Proc. Biol. Soc. Washington, vol. xxi. p. 126.

At Long Island a single small specimen of this comatulid was taken, but it is not typical. The ridge across the segments of the cirri is very inconspicuous, and none of the pinnule segments have conspicuous projections. There are ten arms about 35 mm. long, and the cirri are XII, 17.  $P_1$  has 10 segments,  $P_2$  has the same number but is conspicuously bigger, while  $P_3$  also has 10 segments and is about equal to  $P_1$ . In colour the general impression is olive-cream and purple, the former being the ground-colour. There is a distinct wide purple line up each side of  $Br_1$  and  $B_2$  basally, but this soon breaks up into spots, and disappears in the joints or in lines across the segments at their margins. There is no regularity of arrangement.

The occurrence of *serripinna* at the Abrolhos is unexpected, as it has not been hitherto recorded from Australia, but Mr. A. H. Clark considers this specimen undoubtedly Carpenter's species and not *O. carpenteri* Bell, which has been recorded from northern Australia several times. (A. J. D.)

**ASTEROIDEA.****ASTROPECTEN PREISSII.**

Müller & Troschel, 1843, Arch. f. Naturg., jhrg. ix. 1, p. 119.

There are three *Astropectens*, dredged off Fremantle, which seem to be undoubtedly this species. They have lost all indication of their original colour and are now dingy light-brown. The smallest has  $R = 30$ ,  $r = 6$ , and  $br = 6.5$  mm.; thus  $R = 5r$ . Superomarginal plates all unarmed. Inferomarginals with a single wide, flat, pointed marginal spine, below which are two very much smaller and more slender spines, of which the adoral is smaller; about four somewhat smaller spines form a longitudinal, well-spaced series on the ventral surface of the plate. A second specimen has  $R = 70$ ,  $r = 10$ , and  $br = 13$  mm.; hence  $R = 7r$ . On one arm three of the distal superomarginals bear small but distinct spinelets. The armature of the inferomarginals is essentially as in the young individual, but the marginal spines and those below are markedly heavier. The third specimen has  $R = 120$ ,  $r = 15$ , and  $br = 17$  mm.; hence  $R = 8r$ . There are no superomarginal spinelets, and the inferomarginal armature is also quite typical.

**LUIDIA MACULATA AUSTRALIÆ.**

*Luidia australiæ* Döderlein, 1920, 'Siboga' Ast. pt. ii. Luidia, p. 206.

An adult specimen, taken near Fremantle, has the usual seven rays, and the measurements are  $R = 225$ ,  $r = 29$ , and  $br = 31$  mm. The distal paxillæ are characteristically large, and there are some pedicellariæ on the

lateral paxillæ near the arm-bases. The arms are rather wide near the tip, not tapering so much as in some Chinese specimens. Although I have not seen any really intermediate specimens, I think the Australian form is more probably a local subspecies than a distinct species. Döderlein himself suggests that it should perhaps be considered "nur als eine Lokalform." Material from the northern coast of Australia and the southern East Indies is essential for a proper solution of the problem.

*NECTRIA MACROBRACHIA* \*, sp. nov. (Pl. 13. figs. 5, 6.)

*Diagnosis* : Disk small ; arms relatively long and cylindrical. Granulation of abactinal plates, near tips of rays, coarse, crowded, and prismatic ; actinal granulation noticeably prismatic. Abactinal plates of disk and arm-bases less paxilliform and more crowded than in the other members of the genus.

*Description of holotype* : Rays 5.  $R=60$  mm. ;  $r=17$  mm. ;  $R=3.5 r$ .  $Br=16$  mm.  $Br$  at middle of ray  $=10$  mm. ; at tip, 6 mm. Disk relatively small, only a little elevated ; arms relatively narrow, for the genus, somewhat flattened basally, but nearly cylindrical or terete for the distal half. Abactinal plates on disk and on basal two-thirds or more of rays, large, low, flat, more or less irregularly hexagonal with rounded corners, well spaced but not widely separated, of dissimilar size ; they are connected with each other by heavy radiating ossicles, in the spaces between which arise papulæ in groups of 4-14. Each plate is covered by a coat of low, more or less convex, polygonal granules ; there are about 40-50 on a plate 2-2.5 mm. in diameter, besides a marginal series of about 25 distinctly larger granules. The marginal series of adjacent plates are in close contact even on disk, except here and there at the angles. Distal part of rays covered by similar but coarser granules, quite closely crowded and without indication of marginal series. Madrepore small, about 2 mm. across, situated half-way between centre and margin of disk.

Superomarginal plates about 25, very similar to the abactinal plates in covering and appearance ; interrarial ones much higher than long ; distally and especially close to tip of ray, the superomarginals are so closely crowded against each other, the abactinal plates, and the inferomarginals that they can be distinguished only imperfectly. Inferomarginals about 27, but distal ones very difficult to make out. The whole distal end of the ray is so closely covered with coarse unequal granules that plate limits cannot be distinguished. Intermarginal, and even inframarginal, papillæ are evident near base of ray.

\*  $\mu\alpha\kappa\rho\acute{o}\varsigma$ =long +  $\beta\rho\alpha\chi\iota\omega\nu$ =arm, in reference to the characteristically long and relatively slender arms.

Actinolateral areas small; along the mid-interradial lines there are about six series of actinolateral plates, but the outermost consists of only one or two plates, the next two are little longer, the next is perhaps 10 mm. long, the second series does not quite reach the middle of the ray and the first extends far out, almost to the tip of the ray; all these plates are covered by coarse prismatic granules, much coarser than those of the abactinal surface; the largest and most prismatic granules are nearest the oral plates.

Adambulacral plates more than 50, the distalmost hard to distinguish; they form a slight undulating margin to the furrow; each plate carries 3 furrow spines (distally only 2), which are subequal, not notably prismatic, blunt, and slightly thicker at tip than at base; distally, as a rule, the adoral is the smaller of the two; near the base of the arm the spinelets are about 2 mm. long, and 50–70  $\mu$ m. thick at tip. On the surface of each adambulacral plate are 3–5 very short, thick, and prismatic spines; the two largest of these adjoin the furrow spines, while the remaining 1–3 are near and resemble the prismatic granules on the first series of actinolaterals. Oral plates not conspicuous or peculiar; even the oral spines are no larger than those on the adjoining adambulacrals. No pedicellariæ were seen anywhere.

Colour light yellowish-grey.

There are two specimens of this interesting new *Nectria*, collected along the shore in the "Pelsart group"; one label says "Pelsart Island." The interbranchial septa are calcified, and the general appearance is so much like *Nectria* that there can be little question of the generic position. And yet the abactinal plates are much less paxilliform, and are much more crowded on the disk and arm-bases than in the other members of the genus. The disk is also very distinctly smaller, and the arms are narrower at base, wider at tip, and more nearly cylindrical than in either *N. ocellata* or *N. ocelligera*. The granulation of the actinal plates, especially at the base of the arms, is noticeably prismatic in *N. macrobrachia*, and that of the abactinal plates at the tips of the rays is coarse, crowded, and prismatic; these differences in granulation, which seem trivial when put into words, are very conspicuous when specimens are compared.

The paratype of *N. macrobrachia* is a badly injured individual, much smaller than the one described. There are but three rays; two, side by side, seem to have been bitten off very close to the disk, apparently at different times, as they show different degrees of healing. The rays present are strongly curved and contracted, but apparently  $R=42$  mm. and  $r=11$ , so that  $R$  is almost 4  $r$ . The granulation and colour are exactly the same as in the holotype. The armature of the adambulacral plates is also similar, but the number of furrow spines is not reduced to two until almost the very tip of the arm is reached.



**PENTAGONASTER STIBARUS.**

H. L. Clark, 1914, Rec. Austral. Mus. i. p. 136.

Two little pentagonal sea-stars from Pelsart Island appear to be the young of this species. The smaller is 17 mm. across,  $R=9$  mm., and has 73 flat abactinal plates besides the madreporite, 4 superomarginals on each side, and a terminal plate on each ray, 99 plates altogether abactinally. The distal marginal plate on each side of each ray is the larger, but is not conspicuously enlarged. Orally there are 4 inferomarginals on each side, and the distal ones on each ray are noticeably larger than the proximal. There are 12 (on 2) or 13 (on 3) plates on each of the interradial areas, and there are 17 adambulacral plates on each furrow margin. The other specimen is a trifle larger (18.5 mm. across), but has only 55 flat abactinal plates besides the 20 marginals, 5 terminals, and madreporite, 81 plates altogether on the dorsal side. On the ventral surface there are 14 (in one area 15) plates in each interradial area. A few pedicellariæ occur on the abactinal surface of each specimen, but there are none on the oral surface.

That these little sea-stars are really the young of *stibarus* seems clear as a result of comparing them with the young of *P. dübeni*. The latter have the abactinal plates swollen, the rays longer and narrower, and, at least in some cases, actinal pedicellariæ are present.

At Wooded Island a larger specimen of *P. stibarus* was taken, 27 mm. across,  $R=15$  mm. There are only 4 marginal plates still in each series, on each side of the distinctly pentagonal sea-star; the distal plate is distinctly the larger in every case. In a specimen of *P. dübeni* of the same size there are 40 superomarginals and 50 inferomarginals, 8 and 10 respectively on each side of the animal, which is not, however, at all pentagonal, since  $R$  is 15 mm. and  $r$  only 8 mm.

**STELLASTER INCEL.**

\* Gray, 1847, Proc. Zool. Soc. London, pt. xv. p. 76.

Two specimens of this well-known sea-star were dredged off Long Island. The larger specimen has  $R=90$  mm. and the smaller 80 mm. There are 2-4 low, blunt spine-like tubercles on the carinal line, on the disk at the base of each arm. The number and arrangement of the inferomarginal spines show great diversity; whereas the number of inferomarginal plates is about 17 in each series, the number of spines ranges from 3 to 11. The present specimens have lost all colour.

**ANTHENEAE AUSTRALIÆ.**

Döderlein, 1915, Jahrb. Nassau. Ver. f. Naturk. Wiesbaden, lxxviii. p. 52.

Two *Antheneae* may well be referred to this species. The genus is a perplexing one, and Döderlein's revision of it is a very admirable piece of

work. His recognition of this species seems to be amply justified. The smaller of the two specimens at hand has  $R=33$  mm. and  $r=15$ , while the larger has the measurements 65 and 30 mm. respectively. Even the latter is only three-fourths as large as Döderlein's type. According to the label the smaller specimen was "dredged between Rat and Pelsart Group." It differs from the larger in the paucity of granules and pedicellariæ on the abactinal surface, which is nearly smooth. Even the superomarginal plates have very small groups of granules, especially near the interradius. At the base of each arm, on the carinal line, 7 mm. from centre of disk, is a low but conspicuous tubercle. There are two smaller tubercles near the anus. Similar tubercles can be seen in the larger specimen, but as they have not increased in size with the growth of the sea-star, they are no longer conspicuous among the numerous granules and pedicellariæ with which the abactinal surface is covered. This larger specimen was dredged off Fremantle. Its colour (dry) is brown-olive, with granules, tubercles, and pedicellariæ nearly white or at least very light brownish and the madreporite chocolate-brown; on the oral surface the granules and pedicellariæ are so numerous and crowded that the general effect is much lighter than dorsally. The smaller specimen is grey-brown above and light yellowish-brown below. The larger specimen is very similar to specimens of *A. pentagonula* of the same size, but it is evidently still immature.

#### ANTHENEAE GLOBIGERA.

Döderlein, 1915, Jahrb. Nassau. Ver. f. Naturk. Wiesbaden, lxxviii. p. 50.

A very fine *Anthenea*, taken by "shore-collecting, Wallaby Group," is undoubtedly to be referred to this well-marked species. It is larger than Döderlein's type, in which  $R=59$  and  $r=30$  mm., for  $R=70$  and  $r=34$  mm. The radial series of tubercles is nearly wanting, though the 5 primary ones are evident. Large dorsal pedicellariæ are numerous and conspicuous. The tubercles on the marginal plates are smaller than in Döderlein's type. The dorsal surface is dark purple-brown, with tubercles, pedicellariæ, and madreporite conspicuously light-coloured in contrast; the oral surface is wood-brown, the tubercles, spinelets, and pedicellariæ much lighter.

#### FROMIA ANDAMANENSIS.

Koehler, 1909, 'Investigator' Ast. p. 105.

Six specimens of a *Fromia* have been a source of great perplexity in the study of the Abrolhos sea-stars, but I have failed to find any satisfactory reason for not referring them to *andamanensis*. The unique holotype of that species is from the Andaman Islands, without more definite locality, and while it is recorded as from "238-290 fathoms," I think there is undoubtedly a mistake about the depth. (Certainly the specimens from the

Abrolhos are typical littoral sea-stars. None is exactly like Koehler's figure of *F. andamanensis*, but the one most like it is only a trifle larger and has the rays just a little bit more slender. The abactinal plating is very much as Koehler shows it, but the rays are not so flattened. This specimen was taken at Pelsart Island, and no two of the rays are the same length. The longest has  $R = 32$  mm., the shortest only 17. The colour is very light, almost a dirty whitish (dry). A specimen of about the same size from "Wallaby Group. Shore" is brown in colour, and the abactinal plates are no more numerous than in the Pelsart specimen. At the base of the ray one can count six or perhaps seven longitudinal series of these plates. A larger specimen from the Wallaby station has  $R = 35$  mm., and there are nine or ten series of abactinal plates, which are noticeably smaller and of more uniform size than in the other specimen. In this larger specimen the rays are nearly equal, only one being noticeably shorter than the others, and they are distinctly terete and not flattened, the height at the base being 9 mm. and the width 11. The colour is brown as in the smaller specimen. Shore-collecting at Long Island yielded an individual very much like those from the Wallaby Group with  $R = 35$  mm., but having the rays a trifle more flattened ( $11.5 \times 8.5$  mm.). Dredging off Long Island yielded a slightly larger specimen, in which the longest  $R = 40$  mm., but  $br = 10$  mm. and height of arm at base about 8 mm. This specimen is also much lighter coloured, nearly white. Finally, from the reef-flat at Pelsart Isle is a much larger *Fromia*, with  $R = 54$  mm.,  $br = 12$ , and height of arm at base only 7 mm., of a pale brown colour and having 10 or 11 longitudinal series of abactinal plates. The disconcerting feature of this specimen is that many of the adambulacral plates on the basal half of the rays have three furrow spines. Thus the flatness of the rays and the adambulacral armature approach closely to *F. milleporella*. On the other hand, the large number of series of abactinal plates and the more slender rays give this large *Fromia* a different facies from ordinary *F. milleporella*, and taken in connection with the presence of only two furrow spines on most of the plates, warrant us in considering *F. andamanensis* as a distinct species. Information regarding the colour in life would perhaps be decisive, but the labels with the present specimens are blank on that point.

#### FROMIA ELEGANS.

II. L. Clark, 1921, Echinoderm Fauna of Torres Strait, p. 43.

There are two *Fromias* in the collection which are labelled "Colour—Brown dark. Locality—1st Island. Dredge." The smaller has all the rays broken; it resembles the small specimen of *F. andamanensis* from Pelsart Isle, but the abactinal plates are noticeably larger. The other specimen is perfect and has  $R = 40$  mm.,  $r$  and  $br = 10$  mm. The disk and rays are quite flat, the height of the arms at base being only about 6–7 mm.

I cannot find a single reliable character by which to separate this specimen from *F. elegans*, yet the abactinal plates are not so large or well defined as in that species. The coloration is now pale brownish, but in life it must have been very similar to that of *F. elegans*, if we may trust the label. On the whole it seems better to refer these two specimens from "1st Island" to *F. elegans* than to include them under the name *F. andamanensis*.

#### BUNASTER LITHODES.

W. K. Fisher, 1917, Proc. Biol. Soc. Wash. xxx. p. 91.

There are four little ophiasterids in the collections, two from Pelsart Island and two from Wooded Island, which undoubtedly belong to the genus *Bunaster*. They are certainly not *B. ritteri*, for pedicellariæ are present and there are no "ball and socket" plates, and they are not *B. uniserialis*, as comparison with the holotype of that species shows. After very prolonged study it seems best to consider them as young *B. lithodes*, in the holotype of which species  $R = 22$  mm. In none of the Abrolhos specimens does  $R$  exceed 10 mm. The most noticeable resemblance between these specimens and *B. lithodes* is seen in the finely shagreen-like covering (aside from the abactinal plates) of the upper half of the animal; in *B. uniserialis* the space between the abactinal plates is occupied by a coarse granulation, as it is in *B. ritteri* also. In two points the Abrolhos specimens are unlike *B. lithodes*; the subambulacral spines are very little longer than broad, and it is hard to see more than a single row of actino-lateral plates even at the base of the arm. These two points may be dependent, however, upon maturity, and the characters are certainly liable to growth-changes. In view, then, of the obvious immaturity of these little Bunasters, I think they may well be referred to *B. lithodes*.

The two specimens from Pelsart Island have  $R = 8$  or 9 mm. They are shell-pink, faintly variegated with whitish and decidedly lighter below than above. One of the Wooded Island specimens has  $R = 9$  mm., and the rays are distinctly more slender than in the others. Its colour is also a very much darker pink. The fourth specimen has  $R = 10$  mm.; the rays are stout and the pink colour has been entirely bleached.

#### PETRICIA OBESA \*, sp. nov. (Pl. 13. figs. 1, 2.)

*Diagnosis*: Rays wide, rounded at tip. Abactinal skeleton concealed by the very thick skin with which it is covered. No tuberoles, spinelets, or even granules on distal marginal plates.

*Description of holotype*: Rays 5.  $R = 65$  mm.;  $r = 30$  mm.;  $R = 2.17r$ .  $Br = 32$  mm.  $Br$  at middle of ray = 24 mm.; at 5 mm. from tip, 15 mm. Disk large, only slightly elevated; arms wide, slightly arched, very blunt

\* *Obesus* = fat, in reference to the wide, blunt rays and the thick skin.

and rounded at tip. Abactinal skeleton almost completely hidden, even in the thoroughly dry specimens, by the very thick skin which covers the whole animal. Papulae numerous, in large irregularly-defined and more or less coalescent groups, absent only from the terminal fifth of the rays. Anus well marked by the fine calcareous papillae which surround it, nearly central in position. Madreporite 10 mm. from anus, small (2 mm. across) but distinct. Interradial pedicellariae huge and very conspicuous, the valves 4-5 mm. long. No other pedicellariae are present.

Marginal plates almost completely concealed by the thick skin; the infero-marginals appear to be larger than those of the upper series, and are larger distally than interradi ally; there are about a dozen in each series. They bear no spinelets, nor is the surface at all rough or shagreen-like. Interradial areas covered by thick, smooth skin, through which one can distinguish some actinolateral plates, of which the series adjoining the furrow reaches to about the middle of the arm. Adambulacral plates about 50 on each side of the furrow; each plate carries two (rarely three and even more rarely only one) spines, 2-2.5 mm. long, shaped like a bowling-pin, blunt, and even a little capitate at the tip. These spines are connected clear to their tips by a fleshy fold of skin. Outside this fold is the series of subambulacral spines, which are stouter than the furrow spines and are buried nearly to their tips in skin, though in the distal part of the ray they are more free. On some plates at the base of the arms there are two subambulacral spines, but as a rule there is a single one on each plate. Oral plates are not distinguishable, but they carry five, rarely six, spines on each side of the jaw, the most proximal largest, about 3 mm. long. On the surface of the jaw are four short, thick spinelets, two on each side, one proximal, one distal, buried in skin, and very similar to the subambulacral spines. Colour (dry) dull chocolate, of somewhat varied hues, the darker with a purplish cast; adambulacral spines and jaws of interradial pedicellariae, nearly white.

There are two specimens of this remarkable sea-star from Pelsart Island, but they differ so much from each other in colour that it is hard to believe they are of the same species. Unfortunately the labels say nothing as to the colour in life, so we do not know how much of the present difference may be artificial. The paratype is dull greenish-yellow; everywhere the outer surface layer of skin has cracked, permitting the deeper layer, which is nearly white, to show through. This is particularly marked on the actinal interradial areas. The interradial pedicellariae are smaller and much less conspicuous in the paratype, but there are no other differences worth noting. The size is essentially the same.

The occurrence of *Petricia* on the western side of the continent is very interesting, but the Abrolhos species is very different from *P. vernicina*, the species which occurs at Port Jackson and along the southern coast. The

chief points of distinction are the wider and terminally rounded rays, the thick skin which conceals the skeletal plates and is not at all smooth and shiny when dry (the feature from which *P. vernicina* gets its appropriate name), and the absence of tubercles, spinelets, or even granules on the distal marginal plates, in *P. obesa*. The West Australian species seems to be somewhat larger than the one from the east coast, the largest specimens of which have  $R=50-60$  mm.

#### ASTERINA BURTONII.

Gray, 1840, Ann. Mag. Nat. Hist. vi. p. 289.

There are half a dozen very typical specimens of this little sea-star, one dredged off Long Island and the other from Wooded Island. The largest has  $R=26$  mm. None of the specimens has retained any of its natural colour. The discovery of this species at the Abrolhos extends its known range very far to the south on the Australian coast.

#### ASTERINA GUNNII.

Gray, 1840, Ann. Mag. Nat. Hist. vi. p. 289.

There is a badly damaged small specimen ( $R=27$  mm.) of this southern species in the collection, but it is not from the Abrolhos. It was dredged off Garden Island near Fremantle, which is probably about the northern limit of the species on the western coast.

#### PARASTERINA CRASSA Fisher. (Pl. 13. figs. 3, 4.)

*Patiria* (?) *crassa* Gray, 1847, Proc. Zool. Soc. London, p. 83.

*Parasterina crassa* Fisher, 1908, Smithsonian Misc. Coll. lii. p. 90.

A sea-star dredged off Fremantle is apparently to be referred to this species, as it answers well to Perrier's (1875, Arch. Zool. Exp. v. p. 142) rather detailed description except for its much larger size. Gray makes no reference to the size of his specimen, but Perrier says " $d=10$  mm." From the context one would infer that  $d$  meant the distance from tip to tip of alternate rays—that is, the diameter of the entire animal; but in that case the specimens in the British Museum are tiny indeed, and it seems incredible that the description given could apply to so small an individual. If  $d$  refers to the diameter of the disk, then Perrier's specimen was only about half as large as the one in hand. Possibly the 10 is a misprint for 100, but in that case the present specimen is much smaller than those in the British Museum. Perrier refers several times to resemblances to *Pentanogaster*. These led me for a time to feel sure that my specimen could not be *P. crassa*, as I see nothing in which it is the least like *Pentagonaster*, save possibly the ambulacral armature, where a slight resemblance might be imagined.

The present specimen has  $R=36$  mm. and  $r=9$ , and  $R$  is therefore equal to  $4r$ ; Perrier says  $R=3\frac{1}{2}r$ , a difference easily understood if his specimen had  $r$  only 5 mm. Perrier says that the large ossicles in the dorsal skeleton

are more numerous than the small ones, and then says the papulæ are surrounded by the small ones, which certainly implies a considerable number of the latter. In the present specimen, near the base of the arm there are about five small plates to each one of the large ones. At the tips of the rays, however, the large plates become more numerous. All plates, both on the dorsal and oral surfaces of the sea-star, are closely covered with cylindrical spinelets like those occurring in *Asterina*. Dorsally the spinelets end in 2-4, usually 3, glassy points of which one is larger than the other; ventrally there are more glassy points on each spinelet, and they are subequal. Even on the ventral plates, I cannot see that these crowded spinelets resemble a "granulation" as Perrier says. Gray says the colour of his dry specimen was pale yellow, and the one before me might be called dirty yellow. Perrier says that some of those in the British Museum were "encore variés de jaune et de blanc," but immediately states that the spines on the large ossicles were "bleus"; probably either "blanc" or "bleus" is a typographical error.

#### COSCINASTERIAS CALAMARIA.

*Asterias calamaria* Gray, 1840, Ann. Mag. Nat. Hist. vi. p. 179.

*Coscinasterias calamaria* Perrier, 1894, 'Travailleur' et 'Talisman' Stell. p. 106.

A sea-star dredged near Fremantle is the only representative in the collection of this characteristic species of southern Australia. It is a small specimen in poor condition, only three arms remaining attached to the disk, which is but 10 mm. across. The rays are about 55 mm. long, and there evidently were eleven of them originally.

#### UNIOPHORA DYSCRITA \*, sp. nov.

*Diagnosis*: Disk moderate, little elevated; arms short, wide, and little arched. Inferomarginal, actinal, and adambulacral spines flattened, chisel-like at tip. No intermarginal plates. No shagreen-like areas on superomarginal plates. Abactinal spinelets of two kinds, blunt cylindrical and capitate conical.

*Description of holotype*: Rays 5.  $R=55$  mm.;  $r=13$  mm.;  $R=4r+$ .  $Br=15$  mm.  $Br$  at middle of ray, 13 mm.; at 5 mm. from tip, 7 mm. Disk moderate, little elevated; arms wide and little arched. The specimen is dry and flattened, and it is hard to tell how much elevated and arched the upper surface may have been in life. Abactinal skeleton of rather heavy plates forming an irregular and very open network, the meshes of which are four distinct series only at the base of the arm; at the middle of the arm the lateral series are still evident, but the median series are quite replaced by irregularly-arranged meshes 3-5 mm. across, more or less occupied, at least at centre, by papulæ. Basally there are 4-12 papulæ in the mesh-areas.

\* *δύσκριτος*=hard to determine, in reference to the difficulty of distinguishing the species of *Uniophora*.

Marginal plates very distinct, the upper series forming a very evident boundary to the abactinal surface of the arm. Intermarginal papulae numerous. At the base of each arm a carinal series of plates is evident and one lateral series on each side, but on most of the abactinal surface of each arm, as well as on the disk, there is no definite arrangement of the plates evident. Most of the abactinal and superomarginal plates carry spinelets and minute pedicellariae. The latter are scattered and not very numerous. The spinelets are of two sorts: nearly cylindrical very blunt ones about .50-.75 mm. long and the diameter one-third to one-half as much; and stout, markedly conically capitate spinelets 1-1.5 mm. long and about one millimetre in diameter; on the marginal plates these heavy spinelets are conical rather than capitate. There is never more than one of the stout spinelets on a plate, but one finds on each side of it, usually, 1-3 of the more slender little spinelets; occasionally the stout spinelet is solitary. On the more conspicuous abactinal plates the spinelets form transverse series, sometimes without any large one at the middle. Madreporite 2 or 3 mm. from the disk margin, small, scarcely 2 mm. in diameter, elevated and surrounded by a circlet of 15-20 small spinelets.

Inferomarginal plates about 28, each with a stout spine, rarely accompanied by a single much smaller one; distally the spines are low, blunt, conically, but proximally they are flattened and the tips are chisel-like, or deeply channelled on the upper side, or divided into 2 or 3 very short branches. These proximal spines are about 2 mm. long with the tip a millimetre or more wide. Actinolateral spines in two series continuing nearly to tip of ray; at base of arm there seem to be two series of actinolateral plates, but it is hard to determine how far out on the arm they are continued; the spines are similar to those on the inferomarginal plates, but are smaller; there is seldom more than one to a plate. Adambulacral spines about 2 mm. long, flat, blunt, and rounded, or a little widened at tip, in two regular crowded series; the spines of the outer series are only a little, if any, larger than those next the furrow. Oral plates, each with three spines of which the distal is smallest and most like the adambulacral spines, while the most proximal is 3 mm. or more long and very flat and chisel-like. Tube-feet crowded, in four series. Pedicellariae are very few on the actinal surface; here and there are scattered minute forcipiform pedicellariae, and near the base of the ray careful search reveals a few small forcipiform pedicellariae, with short, erect jaws and no stalk; they are about as wide as long.

Colour, of dry specimen, dull yellowish-grey.

One specimen dredged at Garden Island, near Fremantle.

In view of the confusion already existing in the genus *Uniophora*, it may seem of doubtful utility to describe a new species based on a single specimen, but after examining a considerable number of *Uniophoras* from South Australia, representing at least two species and perhaps more, I am satisfied that this West Australian form is at least distinct from any of those hitherto



described. It is particularly characterised by very flat chisel-like infero-marginal, actinal, and adumbulacral spines, but another feature in which it differs from South Australian specimens is the absence of shagreen-like "pebbled" areas on the lower part of the superomarginal plates. These are quite conspicuous in most of the specimens from South Australia, but can barely be distinguished on one or two plates of the specimen from Garden Island. It should also be mentioned that the present specimen does not seem to have any intermarginal plates, such as occur in some *Uniophoræ*. None of the South Australian specimens have the grey colour of *U. dyscrita*, but, owing to the poor condition of the type, this may be of no significance at all.

### OPHIUROIDEA.

#### EURYALE ASPERA.

Lamarck, 1816, *Anim. s. Vert.* ii. p. 538.

A single specimen of this "basket-fish," 20 mm. across the disk, is labelled as having been brought from Broome. It is very light-coloured, possibly somewhat bleached, but is otherwise in good condition. The species was previously known from north-western Australia only from two young specimens taken by the 'Gazelle.'

#### OPHIACTIS SAVIGNYI.

*Ophiolepis savignyi* Müller & Troschel, 1842, *Syst. Ast.* p. 95.

*Ophiactis savignyi* Ljungman, 1867, *Öfv. Kong. Vet.-Akad. Förh.* xxiii. p. 323.

A single specimen of this tropicopolitan species is in the collection from Wooded Island. It has six arms and the disk is 3 mm. across.

#### OPHIOTHRIX MICHAELSENI.

Koehler, 1907, *Fauna Südwest-Australiens: Ophiuroidea*, i. p. 250.

While I do not feel at all sure of the validity of this species, since the section of the genus to which it belongs is in very great confusion, there is a specimen of *Ophiotrix* at hand, taken at Garden Island near Fremantle, which is almost certainly identical with Koehler's specimens and may well bear their name until the group is revised. It is 13 mm. across the disk, and although the arms are all broken, enough is left (65-115 u.m.) to show that they are very long. The disk is grey, the arm-spines pale brown, and the upper side of the arms is indistinctly banded with dark and light slate-colour; there is a narrow, more or less interrupted, light line along the middle of the upper-arm surface.

#### OPHIOTHRIX SPONGICOLA.

Stimpson, 1855, *Proc. Acad. Nat. Sci. Philad.* vii. p. 385.

This is one of the few characteristic species of the southern coasts of Australia which occur at the Abrolhos. In the present collection there are

three specimens from "Garden Island, near Fremantle; dredged," one from "off Fremantle," one from "Wooded Isle," and four from "Long Island." None of the specimens is large, the disk diameters ranging from 4 to 8 mm.

#### OPHIOTHRIX STELLIGERA.

Lyman, 1874, Bull. M. C. Z. iii. p. 237.

A single small specimen, from Garden Island, near Fremantle, has the disk only 3 mm. across and the arms about 20 mm. long. Seven larger specimens, from "off Long Island," have the disk  $3\frac{1}{2}$ –7 mm. across. Of these Abrolhos specimens, four show spinelets among the thorny stumps on the disk. All the specimens are much alike in their indistinctive, light greyish- or reddish-brown coloration, and show the white stripe on the upper surface of the arms. In the largest specimen a curious anomaly occurs in that on the proximal part of the arm the white stripe is black. Distally there is a white stripe delimited by a black line on each side, but as this passes towards the base of the arm, the black encroaches more and more on the white, and finally obliterates it altogether, the two black lines coalescing. Were the arms broken off near the base, it would be hard to believe that the brittle-star was really an example of *stelligera*.

#### OPHIONEREIS PORRECTA.

Lyman, 1860, Proc. Boston Soc. Nat. Hist. vii. p. 260.

The occurrence of this species in the Abrolhos is most interesting, as it does not seem to be common anywhere in the East Indies and is not yet known from the mainland coast of Australia, although it is not rare at the Murray Islands, in the Torres Strait region. There are five specimens at hand from Wooded Island and two from Pelsart. One of the latter is only 4 mm. across the disk and has the arms about 20 mm. long. The disk is nearly pure white, save for the dark brown distal tips of the radial shields. The other half dozen specimens are 8–12 mm. across the disk.

#### OPHIOCOMA BREVIPES VAR. VARIEGATA.

*Ophiocoma variegata* E. A. Smith, 1876, Ann. Mag. Nat. Hist. (4) xviii. p. 39.

*Ophiocoma brevipes* var. *variegata* H. L. Clark, 1921, Echinoderms of Torres Strait, p. 130.

It is rather remarkable that this widespread and variable *Ophiocoma* should be the only representative of the family taken at the Abrolhos. It was found both at Wooded Island (8 specimens) and at Long Island, Pelsart Group (4 specimens). The specimens range in disk-diameter from 12 to 29 mm. All are evidently to be referred to the variety *variegata*, but two have the black-spotted disk of the form that has been called *O. döderleini* and two have the reticulated disk of the so-called *O. dentata*. None is like *O. insularia* or the typical *O. brevipes*.

**OPHIOPLOCUS IMBRICATUS.**

*Ophiolepis imbricata* Müller & Troschel, 1842, Syst. Ast. p. 93.

*Ophioplocus imbricatus* Lyman, 1861, Proc. Boston Soc. Nat. Hist. viii. p. 73, footnote.

There are two adults, light-coloured specimens of this species in the collection, taken on the reef at Long Island, Pelsart Group.

**ECHINOIDEA.****PRIONOCIDARIS BACULOSA var. ANNULIFERA.**

*Cidarites annulifera* Lamarck, 1816, Anim. s. Vert. iii. p. 57.

*Prionocidaris baculosa* var. *annulifera* Mortensen, 1918, Kungl. Svenska Vetensk. Handl. lviii. no. 9, p. 8.

A very fine specimen of this handsome sea-urchin was dredged among the islands of the Wallaby Group. It is 49 mm. in horizontal diameter, and the largest primary spines, which are all more or less conspicuously banded with reddish-purple and greenish-yellow, are about 57 mm. long and 5 mm. in diameter near the base. The number and arrangement of the conspicuous red-purple spots on the collar of the primaries show great diversity.

**PRIONOCIDARIS BISPINOSA var. CHINENSIS.**

Döderlein, 1903, Jena Denkschr. viii. p. 697.

A small cidarid dredged off Long Island resembles so closely Döderlein's description and figure that I refer it to this variety with little hesitation, even though the type-locality is so far distant from the Abrolhos. The specimen is 35 mm. in diameter. Most of the primary spines are broken or missing, but the unspotted red-brown collar is characteristic, and the distinctive thorns are well-developed on the upper spines. The longest ones, 33 mm. long, 2 mm. in diameter at the collar, cylindrical, and without thorns, are at the mid-zone. The secondary spines are brownish-red, those on the ambulacra being slightly darker than those on the interambulacra and with a purplish tinge.

**CENTRECHINUS SAVIGNYI.**

*Diadema savignyi* Michelin, 1845, Rev. Mag. Zool. p. 15.

*Centrechinus savignyi* H. L. Clark, 1921, Echinoderm Fauna of Torres Strait, p. 145.

A specimen 85 mm. in diameter was taken in the shore-collecting at Wooded Island.

**CENTRECHINUS SETOSUS.**

*Echinometra setosa* Leske, 1778, Add. ad. Klein, p. 36.

*Centrechinus setosus* Jackson, 1912, Phylogeny of Echini, p. 28.

A specimen 80 mm. in diameter was taken during the shore-collecting in the Pelsart Group. The abactinal white spots are large and conspicuous, and easily distinguish the species from the preceding.

**CENTROSTEPHANUS TENUISPINUS.**

H. L. Clark, 1914, Rec. W. Austral. Mus. i. p. 162.

There are three half-grown but typical examples of this western species, one of which was taken in the lagoon at Pelsart Isle, while the other two were dredged off Long Island.

**AMBLYPNEUSTES PALLIDUS.**

*Echinus pallidus* Lamarck, 1816, Anim. s. Vert. iii. p. 48.

*Amblypneustes pallidus* Valenciennes, 1846, Voy. 'Venus,' Zoophytes, pl. ii. fig. 1.

A small *Amblypneustes* from Wooded Island, about 20 mm. in diameter and nearly 20 mm. high, is best referred to this species, although the diamond-shaped markings on the interambulacra are very faint. The test is faintly pink, the secondary and miliary spines dirty whitish, and the primaries are pale red. There are no spines on the anal system, and the tuberculation of the test is that which is characteristic of *A. pallidus*.

**SALMACIS VIRGULATA ALEXANDRI.**

*Salmacis alexandri* Bell, 1884, 'Alert' Rep. p. 118.

*Salmacis virgulata alexandri* Döderlein, 1914, Ech. Südwest. Aust. p. 454.

This urchin has already been recorded from Geraldton and from Sharks Bay, so the occurrence of two large specimens (74 and 79 mm. respectively in horizontal diameter) from the Abrolhos is not surprising. They were dredged off Long Island. One has a low ambitus and flat oval surface, though the test is fairly high, while the other has a lower test and the ambitus much nearer to the mid-zone. In the latter specimen the primary spines are green, though the test is light purple, only the primaries near the peristome being somewhat purple near the base. In the larger specimen the primaries, as well as the test, are purple, but those below the ambitus are much longer and more brightly coloured than those above, and all are tipped with white.

**PSEUDOBOLETIA INDIANA.**

*Taropneustes indianus* Michelin, 1862, Ech. et Stel.: Année A, in Maillard's Notes sur Bourbon, p. 5.

*Pseudoboletia indiana* A. Agassiz, 1872, Rev. Ech. pt. I, p. 153.

The occurrence of a *Pseudoboletia* on the western side of the Australian continent is a discovery of more than ordinary interest, as the genus has not hitherto been reported from Australia or the Torres Strait region. But the present specimen, 50 mm. in diameter, with a dirty white coloration lacking all indication of pink, is unmistakable. It was dredged off Long Island.

**TRIPNEUSTES GRATILLA.**

*Echinus gratilla* Linné, 1758, Syst. Nat. ed. x. p. 664.

*Tripneustes gratilla* Lovén, 1887, Ech. Linn. p. 77.

Two specimens, 68 and 86 mm. in diameter, with dark test and white

spines, were taken at Pelsart Island, thus extending the known range of the species on the western side of Australia considerably to the south. On the mainland coast it is known only as far south as Sharks Bay.

#### HELIOCIDARIS ERYTHROGRAMMA.

*Echinus erythrogrammus* Valenciennes, 1846, Voy. 'Venus,' Zoophytes, pl. vii. fig. 1.

*Helicoidaris erythrogramma* Agassiz & Desor, 1846, Ann. Sci. Nat. Zool. (3) vi. p. 371

There are half a dozen specimens of this well-known species of the southern Australian coast, but all are young and the specific characters are not well marked. Three from the lagoon, Pelsart Group, 25–30 mm. in diameter and 13–14 mm. high, have purplish tests and bronze-green spines; the largest primaries are 15 mm. long, and not quite a millimetre in diameter at the base. There is little doubt that these are normal *H. erythrogramma*. There is a very similar specimen from East Wallaby Island. Two specimens from Wooded Island have a different appearance, and yet differ more from each other than either one does from the Pelsart specimens. One is about 28 mm. in diameter, scarcely 13 mm. high, and has the tubercles much more conspicuous than in the others. The primary spines are purple, but the secondaries show an evident bronze-green coloration. Most of the primaries are broken, but it is obvious that all were more or less stunted; particularly all the spines above the ambitus are relatively short and thick and blunt. Apparently this specimen lived beneath a rock or among rocks where surf or tidal currents were strong. The other Wooded Island specimen has the test very light-coloured, with a green tinge abactinally, and the spines are green tinged with purple at the tip, at least orally. The largest primaries are 10–12 mm. long, with the diameter at base distinctly more than a millimetre. This individual looks like a different species from the others, and may be a young *H. tuberculata*, but it is highly improbable that that species occurs in the Abrolhos. Probably this little green specimen was collected on an eel-grass bottom in still water, such an environment as favours the green colour and the better-developed spines.

#### ECHINOMETRA MATHAEI.

*Echinus mathaei* de Blainville, 1825, Dict. Sci. Nat. xxxvii. p. 94.

*Echinometra mathaei* de Blainville, 1830, Dict. Sci. Nat. ix. p. 206.

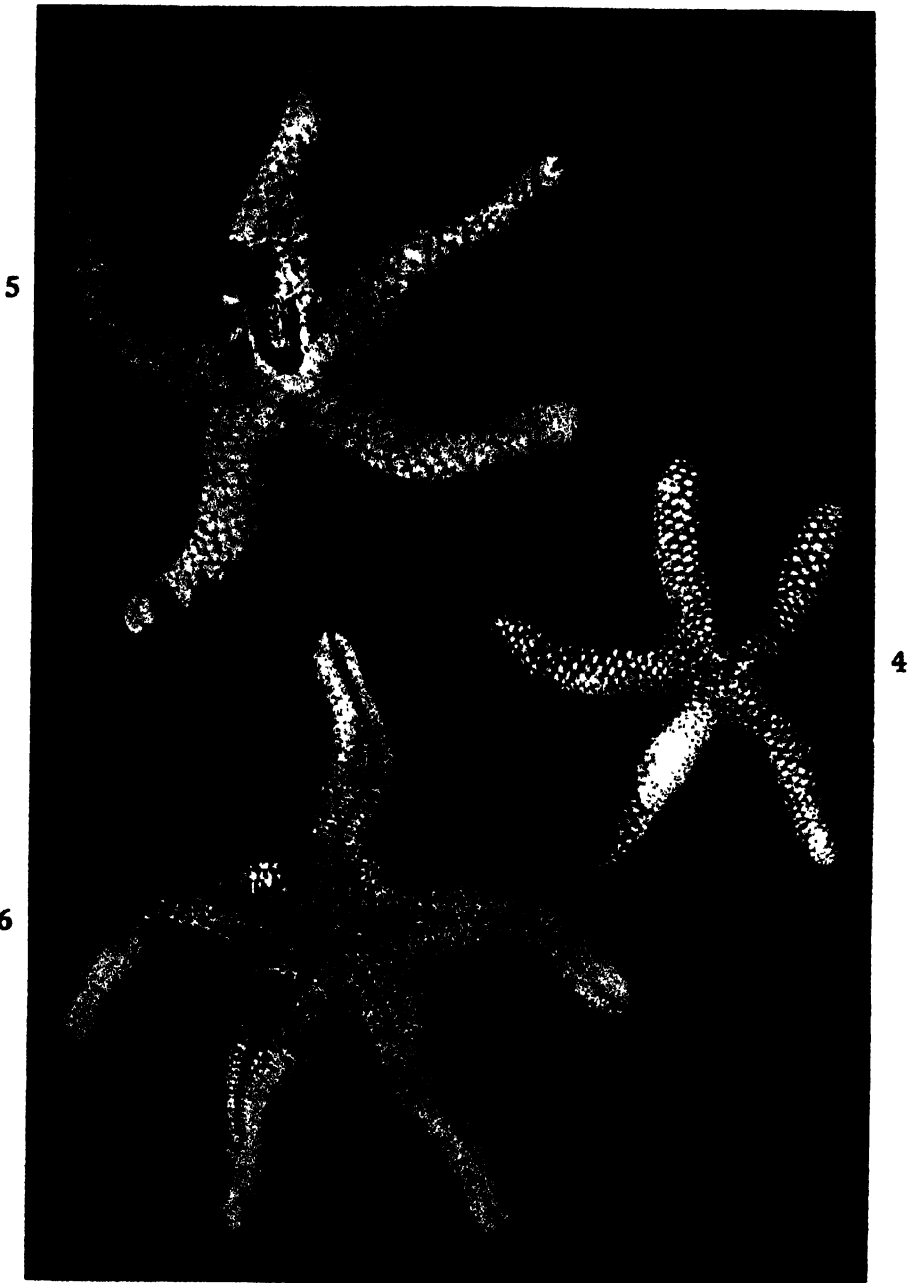
There is a specimen 47 mm. long, 41 mm. wide, and 26 mm. high from North Island, and the label says "Very common everywhere." There are also two small specimens (15–17 mm. long) from "Long Island, shore." The abactinal tube-feet of the large specimen contain large numbers of the triradiate spicules which Döderlein considers typical of his genus *Mortensenia*, but I am not prepared to admit that their presence is even a good *specific* character, and I think these specimens are more properly recorded as *E. mathaei* than as *E. oblonga*. But they are evidently identical with those which Döderlein (1914, Fauna Südwest-Austral. Bd. iv. Lfg. 12, p. 487) identifies as *Mortensenia oblonga*, which were collected in Sharks Bay.





*London, E. & J. Rees, 1911, p. 10, pl. 10, fig. 10*

**ECHINODERMS FROM**



London Stereoscopic Co. Ltd.

WEST AUSTRALIA





**BREYNIA AUSTRALASIÆ.**

*Spatangus australasiæ* Leach, 1815, Zool. Misc. ii. p. 68.

*Breynia australasiæ* Gray, 1855, Cat. Rec. Ech. pt. 1, p. 46.

A single fine specimen from North Island shows that the characteristic species of Australia is not wanting at the Abrolhos.

**ECHINOCARDIUM CORDATUM.**

*Echinus cordatus* Pennant, 1777, Brit. Zool. iv. p. 69.

*Echinocardium cordatus* Gray, 1848, Brit. Rad. p. 6.

Two specimens of this cosmopolitan species are in the collection. They were dredged off Garden Island, near Fremantle. The larger is 32 mm. long, 22 mm. wide, and 13 mm. high.

**EXPLANATION OF PLATE 13.**

Fig. 1. *Petricia obesa*, sp. n., aboral view,  $\frac{3}{4}$ rds nat. size.

2. " " oral view, " "

3. *Parasternia crassa* (Gray) Fisher, oral view, nat. size.

4. " " aboral view, " "

5. *Nectria macrobrachia*, sp. n., aboral view,  $\frac{5}{8}$ ths nat. size.

6. " oral view, " "



Courtship Activities in the Red-throated Diver (*Colymbus stellatus* Pontopp.) ; together with a discussion of the Evolution of Courtship in Birds\*. By JULIAN S. HUXLEY, M.A. (Communicated by Prof. E. S. GOODRICH, M.A., F.R.S., Sec.L.S.)

(PLATES 14, 15, and 4 Text-figures.)

[Read 2nd November, 1922.]

THE following paper is a continuation of previous work on the sexual relationships in species of birds in which both sexes possess bright colours and also exhibit similar sexual ceremonies. The reader is referred to papers on the Great Crested Grebe and on the Dabchick (Huxley, '14 and '19). It is unnecessary to recapitulate at any length, but certain general conclusions may be stated.

1. In most, possibly all monogamous birds, a pre-mating and post-mating period may be distinguished. "Courtship" activities usually occur during both of these periods; but the majority of the "courtship" actions which are to be found described in the literature occur in the post-mating period, and therefore cannot be operative in any true form of sexual selection as imagined by Darwin. So far as pre-mating ceremonies occur and are effective in the choice of mates, they can of course find place in a scheme of true sexual selection.

2. In birds in which the sexes are quite or almost similar, and both adorned with bright colours or special plumes, or other structures, which are displayed or otherwise used in sexual ceremonies, both sexes play a quite or nearly similar rôle during "courtship"; very often ceremonies occur in which both sexes simultaneously play a similar rôle; for such ceremonies the term "mutual" is employed.

3. These mutual ceremonies may be "self-exhausting"—that is, may end in the birds resuming the ordinary routine of life; or they may be a means of raising the emotional tone as a direct or indirect excitant to coition. In the Grebe, where self-exhausting display ceremonies were the rule, special pre-coition ceremonies were found, in which attitudes resembling those employed at coition were adopted.

4. An association of various of the birds' other activities with the sexual ceremonies was often observed. The "handling" of nest-material is frequently so associated, as has been noted by many previous observers; but actions like those of preening or of shaking the head, although originally quite without sexual significance, may also be used as part of the raw material of sexual ceremonies.

\* No. 21 of the Results of the Oxford University Expedition to Spitsbergen in 1921.

5. In many birds similar in the two sexes both male and female incubate. In many but not all such species the relieving of one bird by the other on the nest is the occasion for a special sexual ceremony, which in its turn may or may not be used at other times. This ceremony of nest-relief appears to be absent in the Grebe.

With this brief introduction, we may pass to the observations on the Red-throated Diver. These were made while the writer was on the Oxford University Expedition to Spitsbergen, 1921. Most were made on Prince Charles Foreland, an island 60 miles long, off the west coast, on which a small party of us camped for 11 days, from June 30 to July 10. Numerous small freshwater pools are found here, as in many other places near the coast in Spitsbergen; and on a great many of these, at any rate on the north-western and western coasts, Divers are to be found nesting. We were fortunate in being encamped on the shores of Richard Lagoon, a sheet of brackish water about a mile wide and 5 miles long, communicating with the sea by one narrow opening. This lagoon was the scene of much of the Divers' courtship, both pre- and post-mating, though especially the former. Much of the birds' feeding was done on the open sea: but for rest and courtship the lagoon was chosen. Even after incubation had begun, the birds appeared to come down to the lagoon when not sitting; it was the scene of veritable social gatherings of Divers, four or five being commonly on its waters together, and eight having been seen there on one occasion. Sometimes they would fish, progressing by means of long dives, as does the Crested Grebe; at other times they would stay quiet, resting or preening themselves. But during the period of our stay we never observed two or more Divers on the lagoon without some courtship action following within a comparatively short time. The male and female are similar in appearance; the female is smaller than the male, although the wing and beak measurements of species overlap somewhat. However, the female appears to have a much less massive neck than the male, and a separation of the sexes can usually be made with reasonable probability.

#### *Description of Chief Courtship Actions.*

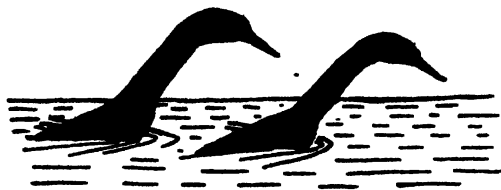
It will be best to begin with a description of the chief types of actions seen, following this with their probable interpretation.

1. "Plesiosaur race." This ceremony was so christened because the attitude adopted by the birds in its performance made them resemble miniature Plesiosaurs half out of water (fig. 1). Usually two or three birds took part in it, sometimes four. The birds depressed the hinder half of the body below the water; the body was held at an angle so that the breast and shoulders were stuck out; the neck was stuck upwards and forwards in a stiff position, the head and beak inclined somewhat forward, again somewhat stiffly. In this attitude the birds swam through the water, accompanying one another.

Their passage through the water seemed to be accompanied by a good deal of resistance, since a wave showed at their breasts. They would go for some distance in this way; then would often turn and continue the process in the opposite direction. The bird which had led in one direction, it seemed, might be replaced by another as leader after turning. The whole ceremony did not give the idea of a true pursuit, such as is seen among many birds, but more of a race, or of something still more ceremonial and formal.

The most usual arrangement is for one bird to lead, the other one or two being half a length or less behind. Various modifications of the pose are seen. Sometimes the body is at a very low angle, the neck little arched, the head and bill almost horizontal; at others the tail is more submerged, the breast more elevated, the neck much arched, and the head and bill pointed downwards; it is in this pose that the likeness to a Plesiosaur is most marked. Occasionally almost the whole of the body is submerged. As to the general appearance, I quote from my notes:—"There is a strange stream-line effect about the creatures. They must be paddling with great energy to keep up

FIG. 1.



Red-throated Diver: Plesiosaurus-race ceremony.

the speed." "There is often a snaky look about them when in the semi-vertical attitude." Altogether the effect as of tension, of emotional ritual, so familiar to all those who have watched birds during courtship, is marked.

A still further modification of the pose is sometimes seen in what may be called the "wing Plesiosaur attitude." In this the wings are stretched out nearly at right angles to the body, perhaps  $2/3$  spread, the point inclined a little backwards, and somewhat drooped, so that the upper surface is plainly visible. This might be adopted by all the birds in a "race," or by the "pursuer" alone in a "race" of two birds only. The same attitudes and relative positions were maintained by one such pair of birds for over 50 yards.

Occasionally birds might be seen in a still more nearly vertical attitude. When this was so they did not progress fast.

A peculiar note invariably accompanied this ceremony. I find it described in my notes as "a growl with a bubble in it" or a "rolling growl." This is repeated a number of times, and appears to be used just before or at the beginning of the ceremony proper. This note did not seem to be used at any other time, except in the "snake-ceremony" (see p. 257).

From the beginning we noticed that birds engaged in this and in other sexual ceremonies, or more often when under the influence of sexual excitement, but not actually engaged in a ceremony, often engaged in curious and apparently meaningless actions. The most frequent was the dipping of the beak in the water (fig. 2), often repeated several times within a few minutes; a variation of this consisted in "looking into the water"—in other words, the submerging of the beak and fore-part of the head for some little time: finally, shaking of the head was observed, though much more rarely than in the Grebe.

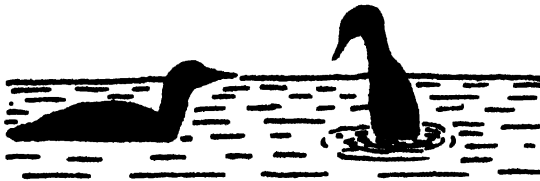
FIG. 2.



Red-throated Diver: snake-ceremony.

It became quite certain, as we continued our observations, that these actions, or at least the two former, were definitely associated with sexual excitement. Like the head-shaking and "habit-preening" of the Grebe (Huxley, '15), they appear to represent actions normally performed with some other function, or, if functionless, with non-sexual associations, which have become, through some peculiarity of the psychological mechanism, secondarily associated with sexual excitement, and used as physical expression of sexual emotion. This appears also to be the case with a special form of dive which I call the "splash-dive." In this, instead of submerging quietly, almost

FIG. 3.



Red-throated Diver: emergence ceremony.

without a ripple, as is done when the birds are diving for food or to escape danger, the bird gives a sharp kick with the legs as it goes under, sending a shower of spray into the air; furthermore, the dive is for a very short distance, the bird emerging generally about 5 or 6 yards away. This, too, is associated with apparently all forms of sexual excitement, and otherwise is used only under the influence of the emotion of anger (see Van Oordt and Huxley, '22). Here we have apparently a normal form of activity, which is used in a modified form when associated with sexual emotion.

2. A very remarkable ceremony, unfortunately only observed clearly on one or two occasions, was the dive followed by vertical emergence (figs. 3 & 4). In the best-observed case two birds out of a party of three were close together. Suddenly one—almost certainly a female—dived (with a splash). The other—almost certainly a male—immediately spread its wings and half flew, half sputtered along the surface of the water for 5 or 6 yards. The bird which had dived then came up out of the water close to the other, in an almost vertical position (fig. 3). The neck was held so as to continue the line of the body; the head bent down so that the bill made a small angle with the breast. The emergence was fairly slow. It stayed in this position for perhaps 5 seconds, then settled down on the water. Here we have a ceremony which is extremely similar to one which I have described in the Crested Grebe, although not quite so elaborate. Its chief feature of interest is that, although both birds play active parts in it (the flying-off and waiting of the non-diving bird is an active part, which culminates in the Grebe with a special display), yet the parts are different. If we may judge from the Grebe, either part

FIG 4.



Red-throated Diver: another sketch of an emergence ceremony.

may at different times be played by a bird of either sex. This is rendered more probable by the fact that the more active rôle on this occasion was apparently taken by a female.

3. A ceremony in many ways resembling the Plesiosaurus race is also common, but apparently only among birds which have mated up. It is always accompanied by a cry which is the same as, or extremely similar to, the "roll-growl" already described. The two birds swim, one leading, for some distance with their necks arched so that the tip of the bill is submerged. The bill is also held open, in order to give the cry. The bodies, however, are not submerged posteriorly, but kept in normal swimming position, and there is not a marked wave thrown off the breast, nor does motion appear to be at all violent. As in the Plesiosaur race, the birds may turn, and the former leader become the second. This ceremony might be performed on the small nesting-pools or on the lagoon. Owing to the snakey look of the neck when in this attitude, I shall call this the *snake-ceremony* (fig. 2).

There remain peculiar actions associated with coition; these, however, may best be described later, in connection with the account of a particular pair.



*Activities of a Particular Mated Pair.*

I will now proceed to describe in some detail the actions of one pair which I had under close observation for a few days, since I believe that in this way a fuller insight is gained by the reader (as it certainly is by the observer at the time) into the psychology of the birds.

On a small tarn about a mile from camp a single Diver was observed on June 30. The tarn was then only partially thawed, and nest-building was out of the question. It would appear, however, that the birds had already "staked out a claim" to this special nesting territory, as is known to be done by many if not all monogamous birds before actual nest-building begins (see E. Howard, '20). A single bird was again observed here on July 4; it was restless and remained on the tarn for a long time; nest-building had almost certainly begun, as the event showed. On July 5 both birds of the pair were seen on the tarn, and one visited the spot where the nest afterwards proved to be. It only stayed half a minute or less, and then returned to the water. The birds were continually giving a mewling call, very similar to that given by solitary birds on the water, or by sitting birds when man or a Skua threatens danger. The call as given on this occasion, however, I record as "louder, longer, and more emotional than when given by a solitary bird." Usually the two birds would howl almost, but not quite, simultaneously. There was certainly some sexual significance attaching to this "duet-howling."

At one moment the typical "roll-growl" was given. This I take as proof that a snake-ceremony occurred, although the birds were unfortunately invisible below the high bank. On my approach to pitch my observation tent, the birds rose together and made off. I take it as certain that no egg was as yet laid, since, once this has happened, the nest is sat on almost continuously to prevent Skuas stealing the egg.

Next day (July 6) I spent about 9 hours at the tarn. It was noticed that whenever the howl or mewling note was given, the neck was stretched out nearly or quite parallel with the water. This was confirmed on many subsequent occasions. The action seems to be inseparable from the particular note. It is probable that it renders the bird less conspicuous (see Van Oordt and Huxley, *loc. cit.*). The note was given repeatedly by the solitary bird (female) that was there at intervals from noon to 3 P.M. Occasionally the bill would be dipped as in sexual excitement. At one time she indulged in what were obviously practice dives, just in and out, emerging two to four lengths away. This was repeated five times in quick succession.

Shortly after, the male arrived. The female speedily joined him, and the pair swam towards me, the female leading, with bill slightly open. When close to the bank, the female suddenly performed a remarkable action, obviously of a sexually stimulating nature. She stretched her neck forwards at an angle of perhaps 30° with the horizontal, the head and beak also

pointing up, but at a less angle. The neck itself was straight and rigid. In this pose she swam close up to the male, crossing his bows, so to speak. Whatever its significance, the performance was exciting to watch. There was a tenseness about the bird's attitude, a rigidity, which has been commented on by other writers, notably by E. Selous, in connection with various sexual ceremonies in other birds (Selous, '01-'02, '05 *a*, '05 *b*). I can best describe the impression it made on me by saying that it was like that apparently produced by certain sexual dances of savage tribes—the whole thing fraught with the significance of sexual emotion, and mysterious in the sense of being thus emotionally charged far beyond the level of ordinary life, but completely natural and without restraint. It is fairly clear that, even in animals, the emotional tension during sexual excitement is far higher than at almost any other time, and that the impression given to the observer is, therefore, not wholly a subjective one.

On this occasion the male was absolutely unresponsive to the female's "stimulating" action. The pair went off together; after some time the female started to go by a long route across dry land to the nest, but soon gave it up. The pair then swam, the female again leading, to a little bar covered with moss on the far shore. This bar I afterwards examined, and found that on it there was a rudimentary nest, built almost entirely of the moss which was here abundant, both on the bar and under the surface of the shallow water near by. Another such "nest" was found on the shore of a second tarn on which a second pair was breeding. Very similar structures are built by the Crested Grebe; and in both cases their function appears to be the same—they are the places on (or near) which the act of coition occurs. Just before arriving here both birds simultaneously "looked into the water" (*vide supra*) for about 20 seconds; there was also a good deal of beak-dipping by both male and female. On arriving at the bar the female turned and gave an energetic splash-dive. The male responded by a less energetic splash-dive. The male then crawled out on the mossy bar, onto what I later found to be the pairing-nest; there he stood upright, stamped alternately with his two feet several times, and then sank down as if brooding. He plucked small fragments of moss in his beak, and apparently placed them round himself as if adding to the nest. The female meanwhile was swimming close to the bar, in water scarcely deeper than her draught, giving repeated splash-dives. Her tail (which of course was very short, as in all Divers and Grebes) was repeatedly wagged up and down. The association of this motion with copulation in birds is obvious and well-known. However, she did not land, but swam across to the right and back, giving several more splash-dives; the male got up and scrambled back into the water. The pair then went to the nearest point to the true nest, both diving twice *en route* (not splash-dives); the female led, at a fast pace. After one short abortive excursion overland towards the nest, followed by swimming off the shore, she

went right up to the nest and settled down on it. The male dozed on the open water with his head under his wing. It was remarkable that since the arrival of the male not a single sound had been uttered by either bird.

About half an hour later the male flew off. The female continued to brood. At one time a Richardson's Skua came down close to the nest. This was the signal for the Diver to give a series of mewing calls, with neck outstretched in the direction of the enemy. (Occasionally the neck may even be directed slightly downwards.) About 7 P.M. I went off to carry out some other work. On returning, she was on the tarn. I visited the nest; and found it a low heap of mud with a shallow depression, and a moderate amount of moss round the rim. There were also several pieces of slate on it, but it was not clear whether their presence was not purely accidental.

On my returning to the hiding-tent, the bird soon came back to the nest. At 7.45 P.M. the male came back to the tarn. The female continued to sit without making any sign for a few minutes, but then suddenly left the nest and joined the male. Both appeared excited, and "looked into the water" several times in quick succession. Immediately afterwards they both assumed a very poor "snake attitude," with the neck only slightly arched. This lasted but a short time; the female then gave five splash-dives in rapid succession. The pair then indulged in a snake-ceremony, swimming towards me almost parallel, neither markedly leading. It was, however, a poor affair compared with those at full intensity of emotion. They then swam close up to the moss-bank on which was the pairing-nest, the female leading; she swam close in and was obviously excited, but the male did not follow. After both had had a spell of rest on the open water, the male looked up and soon started a "roll-growl" (the first sound given by either bird since his arrival). The female soon joined in, and a typical snake-ceremony followed. They then returned, the female leading, to the moss-bank. The male scrambled out again on to the bank, but at the other end from the nest. He trampled as before, but less often, and settled down, but did not pluck any moss. The female, however, after first pecking at the moss on the bank, turned, put her head under water, and proceeded to pull large pieces of moss up from the bottom. These she then jerked backwards over her shoulder, dropping them carelessly into the water and showing no further interest in them. This she did eight or nine times in quick succession. After pecking up moss, both birds usually gave a sharp, emphatic shake of the head.

The male then got off, made for the shore near the true nest, and sat there some time on the mud. Then both came out onto open water, and a good deal of mewing in duet went on.

The female then led the way to the moss-bank, where (I quote from my notes) "she beached herself, stern just in water, breast on land, head down. The male followed, mounted onto her, standing nearly upright, and copulated or attempted to copulate (it did not look as if he was

successful, but this is hard to judge). He then walked up her body and off her right shoulder (in this whole action behaving very much like the Crested Grebe)."

The female remained perfectly motionless for one or two minutes, in the same extended position; the male, after sitting on the bank for a slightly less time, took to the water. The female then sat up, plucked up pieces of moss as before, but fewer and with less energy, and then joined her mate on the water. After swimming, with the male leading, they turned; the female gave a short flight of a few yards, the male swimming rapidly after her; the male then gave a similar short flight. Both shook their heads emphatically several times (compare the Crested Grebe). After a short time the female got up, followed at once by the male, and both flew off westwards and were lost to sight. This abandonment of the nest with an egg in it was remarkable; possibly they were more upset by the presence of the tent than they appeared to be. In any case, apart from the presence of a pair of birds which may or may not have been the same, for a short time next day, the tarn was abandoned, and the egg fell a prey to Skuas within 24 hours.

Another nest was discovered on a neighbouring tarn on July 7. This already contained two eggs, although this tarn had been still later in thawing than the other, and had ice extending for some distance in from all its margins on July 2. This tarn was within a short distance of camp, and the "roll-growl," signifying the mutual "snake-ceremony," was frequently heard from it (*e. g.* 5.30 A.M. July 9). This shows that mutual "courtship" continues, as in the Grebe, throughout the incubation period. On investigating the banks, a "cock's nest," similar to the one already described but rather more rudimentary, was discovered, also on a rather mossy part of the shore (as a matter of fact, the only mossy part in this tarn); doubtless it, too, subserved the function of coition.

The association of the mossy bar with the rudimentary nest is interesting. The true nest often contains some moss; and the behaviour of the female, above recorded, in plucking up moss from the bank shows that in the Diver, as in many other birds, the handling of nest-material has a sexually emotional association. It is presumably this emotional association which prompts the choice of a mossy bank as the site of the pairing-nest. There is, however, far less nest-material employed than by the Grebes: and accordingly nest-material plays a smaller part in the Divers' sexual ceremonies.

On my arriving at the hiding-tent on the evening of July 9, the female, who was sitting, was rather suspicious, left the nest, and swam about restlessly on the pool for some time. Although alone, she frequently dipped her head half into the water, as previously described, for 5 to 15 seconds. Thus this habit, which is undoubtedly the main "associational" habit of this species, may be associated with other emotions than that of sexual excitement—

in this case, with that of anxiety. It was here evident that it was performed especially when the bird was particularly nervous; for instance, whenever she approached the nest-region. This she did repeatedly, sheering off six or eight times before finally plucking up courage to ascend the nest. The "looking in the water" alternated with a curious action of the wings, first one and then the other being raised very slightly. This was not seen at any other time. The male arrived on the tarn about 6 P.M. The female flew along the water to his neighbourhood, uttering a repeated cooing note. Both made towards the nest, the female leading, swimming very low in the water and cooing; she made one short dive. Both then cooed in unison. No ceremony followed, however, and the female soon went on to the nest. The male shortly afterwards flew off, but returned within half an hour. No excitement occurred within the next hour. After this he several times came up close to the nest, and gave the cooing call, which was sometimes given by the female in response. Soon after this he flew off. Here we have evidence of sexual ceremonies in the morning, but a very "dull evening." Probably the mutual ceremonies are practised less, and less as incubation proceeds.

Next day (the 10th) I was in the tent from 2.45 to 5 P.M. The male did not appear at all. The tent was now pitched at 6 yards from the nest. The bird was markedly less nervous than the day before, but every time that she approached the nest from the open water, she dipped her bill several times before venturing on the difficult overland traverse. This corroborates the interpretation of the "looking into the water" as an expression of emotion. On the 11th, the last day we spent on the Foreland, I spent 12.30 to 2 A.M. at this tarn. The male again did not appear. The female appeared to be sitting whenever I was watching; but there is no doubt that the male is to be found sitting in this species (Witherby, '00, &c.). During this period the three birds previously referred to (p. 257) flew down and, after circling round, alighted on the tarn. All were very alert in expression, and were repeatedly dipping their beaks into the water—i. e. under the influence of emotional excitement. From their sizes, I should say there were two females and one male. After a few minutes they rose, circled round again, and again settled. One separated from the other two. The (apparent) male of these two arched its neck very slightly, as if going into the snake position; on this, the other bird dived and emerged in the vertical "Penguin" attitude, as already described. The immediate fluttering over the water by the remaining bird on the female's diving indicates that this is a regularly-occurring ceremony and that the emergence was expected; the same is true in the Grebe.

The "Penguin" bird dived again, with a splash; but before it had emerged, the other two had both, for some unknown reason, flown off. The diving bird emerged in an abortive "Penguin" attitude, looked round to see

where the other was, and then it, too, rose and followed the others. They all three made off in wide sweeps, and were finally lost to view some miles away.

I take it that these three birds were not yet paired up for the season. Possibly here, as in the Crested Grebe (Pike, '13), some birds do not nest, but continue "courtship" actions throughout the season. The long flight to the tarn and away again so soon after is of interest; it may have been a pursuit; but, if so, it is interesting that the bird which took the chief initiative in courtship on the tarn was probably a female.

*Other Observations on the Red-throated Diver's Courtship.*

Before proceeding further, it will be as well to mention the actions observed by others in the same species. E. Selous ('12) made observations on a family in Scotland, during July, at a time when the young were hatched, and were being looked after by both parents. Although he was watching steadily for over three weeks, he only saw "courtship" behaviour on three occasions. This in itself is of interest, as showing that so long as the breeding-season lasts—*i. e.* at any rate so long as the instinct for caring for the young persists, and possibly until the autumn moult—the possibility of sexual ceremonies appearing in special circumstances will also persist. The observations of Pike ('13) are of interest in this connection. He states that a large percentage of the Crested Grebes on a certain breeding area, although mated up, failed, for some unknown reason, to build or lay in the season when he was there: these birds, and apparently none of the other pairs, continued their well-known mutual courtship late into the season (*i. e.* after the normal time for incubation was over). Facts bearing on this problem are well known in other species; for instance, in many birds, the final liberation of the parents from feeding the young, when these are old enough to look after themselves, is often marked by a recrudescence of various sexual activities. These are similar to the truly epigamic activities of the early part of the season, though they now, of course, have no function. Similarly, in birds which rear two or more broods, there is usually a recrudescence of epigamic ceremonies in the interval between broods. Looking at the matter from an opposite angle, we find that the song of many birds, *e. g.* the Nightingale, ceases immediately the young are hatched—*i. e.* as soon as the male embarks upon the new duty of helping feed the young. Mr. Eliot Howard informs me that in birds such as the Buntings, in which the males occupy territory long before the females arrive, the volume of song in the first period is greater than in the period immediately after the arrival of the females. This has been corroborated for other species, *e. g.* the Blackbird (Dewar, '20).

In a very similar way, the female, on reaching a certain level of endocrine stimulation, will permit and indeed solicit coition; her emotional activity will also find relief or expression in the building of the nest. Coition brings about egg-laying, and nest-building brings about the finishing of the nest;

a new period is thus introduced in which new objects are introduced to the bird. Her excitation, so far as it is determined internally, remains at the same level, but her activities are determined also by the objects presented, and she now begins to incubate. In the absence of nest and eggs she would revert to the behaviour of the preceding stage—coition and nest-building once more, as is shown by the behaviour of birds whose nest and eggs are destroyed after incubation has begun; but in the absence of the internal stimulation by the secretion of the gonad, she would neither brood, nor be eager for coition, nor build a nest.

The annual cycle of a bird is therefore divisible into a series of periods, determined (a) by the state of internal stimulation, (b) by external objects—the presence or absence of mate, eggs, young, &c. These latter will determine the division of the breeding-period into a number of sub-periods. In the third place, (c), an influence on behaviour is exerted by general environment—*e.g.* by the state of the weather, the abundance of food, &c.

So long, therefore, as the internal stimulation persists at the same intensity, the sub-periods will be mainly determined by the external objects presented to the bird. But, while any one sub-period will be characterized by one predominant type of behaviour, the other types of behaviour will be latent in the bird all the time, and may emerge under special circumstances, though rarely, so long as the breeding-season (*i.e.* the secretion of the gonad) continues.

To return to Selous's observations on the Diver. The male had just fed one of the chicks; he then approached the part of the pool where the female and other chick were swimming; the female also swam towards him. On the two birds coming to within a certain distance, both made two short flights towards each other over the surface of the water; each time the flight ended by the birds "as it were walking on the water, as a Penguin walks on the land, bolt upright, with the whole of the white expanse of the under surface . . . showing." It is like "a Penguin running a few steps, and then, for an appreciable period, standing upon the water, the naked legs and feet just hidden by it." On another occasion, the male of another pair was seen to alight on the water on its return from the sea, and to end its alighting in the following manner: it "footed it, for a little, towards another one, presumably its mate, . . . maintaining with the help of its wings the upright Penguin-like attitude."

On the third occasion, the female had started to give a special note with head stretched forward; she then began advancing towards the male in a series of little plunges. This stimulated the male to do the same. Each time the cry was given, the neck was arched and held rigid. They eventually met, and then quieted down.

It is interesting to note that none of the actions recorded by Selous are identical with those seen by me. This is probably due, at least in part, to:

the different period at the time of observation. On the other hand, they are built up out of the same elements.

Bent ('19) says of all the species of Diver, as well as of numerous other Pygopodes, that they migrate in pairs, or at least arrive at the breeding localities in pairs, and select the nest-site as soon as possible. He believes they pair for life. In all species it appears probable that both sexes incubate (although from my personal observations it appears that one bird, presumably the female, takes much longer spells than the other; and see Turner, '13).

Courtney, quoted by Chapman ('22), gives a beautiful drawing of a common courtship ceremony of the North American Loon (*Colymbus immer*), in which one bird rises into the erect position, and runs along the surface of the water in this attitude for some way near another.

Bent (*loc. cit.*) refers to the "maniacal" screeching laughter of this species in the breeding-season.

Seidlitz ('13), writing of the Black-throated Diver, says that each pair has a well-marked and large territory (*Revier*). He states that there are as many unpaired as paired birds; these are birds of one, and possibly of two years of age. He does not mention whether these ever indulge in "courtship" ceremonies. This would be a point of considerable interest.

Bahr ('07) mentions the dipping of the beak into the water when the bird is nervous and afraid to return to the nest. He also, on one occasion only, saw a very remarkable performance by a single Red-throated Diver. The bird ascended to a great height, and then descended headlong, twisting and turning as it did so, the air rushing through the feathers making a noise "like a train." Such descents are, of course, well known in many birds, *e.g.* Rook. They are common in Louisiana Heron, Little Blue Heron, and Snowy Egret on returning to their rookery, and I have on one occasion seen a somewhat similar performance by our common British Heron. It is probable that these actions should be classed as play, and not as courtship.

Hatch, quoted by Bent (*loc. cit.*), states that *C. immer* has a remarkable family habit. When the young are (apparently) well-grown, they sleep with their parents on the pool. In the early morning, before sunrise, the male parent gives a special call; all draw near, and, after a little manœuvring, start to run over the water side by side in a line "at incredible speed," with the wings about a quarter-extended, the whole motive power being derived from the feet. They run thus for about 400 yards, then wheel, and return to the starting point. This is repeated several times and suddenly stops. It would be interesting to have further observations on this extraordinary ceremony.

#### INTERPRETATION.

It will be seen from the above that (as in many, and indeed in most, of even our commoner birds) much remains to be known about the life-history



and especially the relations of the sexes. Those who have opportunity, patience, and a good glass, and are willing to take full notes, will find that steady observation of almost any species of bird at the beginning of the breeding-season, particularly if a single pair can be followed throughout, will bring results which may be of very considerable interest, both from the standpoint of pure biology and also from that of comparative psychology, as well as being in itself a very fascinating occupation.

The following paragraphs must therefore be taken only as a provisional interpretation of the observations which have so far been recorded.

The Red-throated Diver is monogamous; possibly it pairs for life. If it pairs for life, it follows that the pairs will have some form of association even through the winter. In any case, however, a change occurs in spring. Either the loose association of male and female is replaced by a much more intimate one, or else the birds have been really unmated during the winter, and now do separate out into pairs. This must, of course, be the case with birds which have not previously mated. In any event, the change is definite, and warrants the term "pairing-up" which is usually given to it. This change is presumably associated with a change in the reproductive organs, which start to secrete their specific hormones.

The pairing-up appears, at least with some individuals, to occur in the winter haunts. When so, it is followed, probably shortly, by migration, in pairs, to the breeding-grounds, where each pair as soon as possible stakes out a territory for itself. The present species appears to breed on small pieces of water, and probably the territory is, in most instances, coterminous with the nesting-pool.

The fact that the pair migrate together and choose the nest-site and territory together is in strong contrast to the occurrences in such Passeres that have been fully investigated, such as the Sylviidæ and the Emberizinae, in which the males alone stake out territory (Howard, '20), and, if migration occurs, migrate before the females. However, it seems to occur in many *Pygopodes* (Bent, *op. cit.*); and in Herons (unpublished observations of my own), although migration is in flocks, the choosing of the nest-site is undertaken by the pair together.

Although from the evidence of others it appears certain that pairing-up may occur before migration, yet my own observations appear to point to this not being universal. The fact that the "Plesiosaur" ceremony occurred frequently during the first few days of our stay, but later was absent or very rare, as well as the fact that the simplest interpretation of it was that it was concerned with the "choosing" of mates, indicates that probably a good many birds arrive unmated on the breeding-grounds. Possibly (I throw this out merely as a suggestion) the birds which have nested before, pair up in winter quarters, while those which are about to nest for the first time do not do so until they arrive on the breeding-grounds.

The "Plesiosaur" or "race" ceremonies, then, appear to be competitions for a mate. It is of interest to find that when three birds are participating in these ceremonies, their respective sizes indicate that they may be either two males and a female or two females and a male. This is in accordance with the rest of the facts observed about courtship in this species—the two sexes appear to play almost identical (or interchangeable) rôles.

The only occasions when I observed the dive followed by the "Penguin-like" emergence, also seemed to be in this *pre-mating* period. The erect "Penguin" attitude, however, as Selous' observations show, is not only confined to this period, although he does not record diving followed by this attitude.

There is, however, another possible interpretation of the participation of three and four birds in these ceremonies, which may be best understood after a brief digression. In the Buntings, as Mr. E. Howard kindly informs me, during the period while male and female are both present on the territory, but coition and nest-building have not yet begun, every day begins in the same identical way. The male wakes first: later, the female emerges too from her roosting-place: after a short time the male flies at her, eager for coition. She however flies off, and there follows what Howard calls the "sexual flight," when the female, dodging and twisting, is pursued closely in her rapid flight by the male. Eventually the birds seem to get exhausted, and alight. Such pursuit flights are of course well known among many species. What is of special interest, however, is the fact that once the flight has started, it is a source of great excitement to other males in the vicinity, and, although these males may have been long in occupation of territory, and mated, yet one or more will usually join the rightful male in the pursuit. In passing, it should be observed that this instinct of other males to join in the excitement of these pursuits appears to be at the bottom of those undignified skirmishes of the House-Sparrow, in which a single unwilling female is mobbed by a number of males; and see also Bent, *op. cit.*, pp. 186–191, where the Californian Guillemot is described as becoming very much excited at the sight of an act of coition by another pair.

It is conceivable that the Plesiosaur race of the Diver may be a mutual "post-mating" ceremony, essentially identical with the "snake-ceremony" described as occurring later in the birds' history, but, since it takes place before the nest is built and other activities share the birds' mind, differing in its greater intensity. If so, then the participation of three or four birds in the ceremony may be due to others joining in under the influence of excitement—others which are either wholly unmated, or else are mated but temporarily without their mates. Since there were almost always several birds on the lagoon, while the nesting-pools hardly ever had more than a single pair on them, and since further the greater level of emotional excitement in the Plesiosaur ceremony is unmistakable, it would be quite intelligible that the threes and fours were only seen on the lagoon, and only performing in the Plesiosaur, not in the "snake" ceremony.

For the present, however, I prefer to think of these as ceremonies actually connected with mating-up. If so, they are interesting, as they would be, so far as I know, the first pre-mating ceremonies described which were "mutual," in that both sexes played similar rôles. Further observations are urgently needed, not only on this particular point, but on the whole problem of pre-mating ceremonies, especially in species with mutual post-mating courtships.

In any case, the *post-mating* ceremonies are essentially mutual. The commonest is the "snake" ceremony, the incentive to which may, to judge from my observations, be given by either sex. This ceremony, like the pre-mating ones, may often be "self-exhausting" in the sense that, as in the Crested Grebe, it need by no means always or usually lead to coition, but may be followed by a relapse into ordinary non-sexual routine. Here, however, I should like to put on record that further observation on this species and on Grebes has convinced me that such ceremonies may often have a stimulative effect, although that effect may be gradual and in a sense cumulative. It is very common in the Grebe to see a pair repeat a series of mutual ceremonies at frequent intervals, and finally go off in the direction of the nest and pairing-platform; this has also been observed in the same species by Selous, and clearly occurs to some extent in the Red-throated Diver. That in certain circumstances the ceremony may be completely self-exhausting is perfectly intelligible: like the song of most Passeres, the performance of the ceremonies is definitely pleasurable in certain states of emotional tension. Physiologically, it is then performed "for its own sake"; it may or may not, according to various circumstances, have the further biological function of raising the emotion to a pitch at which coition is desired.

On the other hand, there is no evidence that in the Divers there exist special attitudes and ceremonies especially used as a symbol of readiness to pair, as in the Grebe. The approach to the pairing-platform is in itself a symbol of some degree of readiness to pair. The emotion associated with this may apparently again be dissipated by excited actions, such as the pulling of weed from the bottom, and by the ascent of the pairing-platform without actual coition.

The situation of the pairing-platform in a mossy situation is of interest. Moss is often but apparently by no means always used as nest-material, and in any case always in very small quantities; the birds can never handle it in such large amounts during nest-building as they do in the vicinity of the pairing-platform. Two hypotheses might be considered in regard to this. In the first place, it might be a reminiscence, the birds having in the past employed more moss in nest-construction than at present. Or it might represent a specialization; once the divergence between nest and pairing-platform had arisen, and the emotions connected with coition had become attached exclusively to the latter, new ceremonies, based on the handling

of nest-material in the first instance, might have been developed in association with the pairing-platform to a much greater pitch than they had ever been formerly. If this is so, and offhand I am inclined to accept it as the more probable, there has been an evolution of the pairing-platform and the ceremonies connected with it, which is in many ways similar to that of the Bower-birds' bower.

Personally I have not seen nearly so many post-mating ceremonies in this species as are to be observed in the Crested Grebe. This is undoubtedly due in part to the paucity of my observations. The work of Selous shows that "Penguin" ceremonies do occur in this period, and, it is interesting to note, continue, though rarely, after the young are hatched. Thus the physiological state (presumably dependent on gonadal secretion) during which epigamic ceremonies can be performed extends, apparently in all birds, up to the very end of the breeding-season; it does not then issue so frequently in "courtship," because incubation and the care of the young afford other outlets for physical energy and emotional tension.

On the other hand, only three, or possibly four types of epigamic ceremony, whether pre- or post-mating, have been observed at all in this species, whereas in the Grebe six have been seen; and the greater abundance in the latter is probably not only apparent but real, and associated with the greater development of epigamic ornament in the Grebe.

Incubation appears to be undertaken mainly by one bird, the smaller of the pair; but there are numerous records of males also incubating, and it is probable that in the Divers, as in other forms with mutual courtship, there is a sharing of the duties of incubation as well as those of caring for the young. It is noteworthy that no ceremonies associated with nest-relief have been observed in the Divers or Grebes, whereas they are common in Herons (my own observations), Pelicans (Chapman, '08), &c. It would be important to find out the range of size in male and female Divers. I am inclined to believe that a single bimodal curve would be obtained. For a discussion of sex-difference in birds with close similarity of male and female, see Huxley, '22 b.

#### GENERAL DISCUSSION.

It remains to discuss some of the general significance of such forms of mutual courtship as are seen in the Divers, Grebes, Herons, and Egrets—to mention only birds whose sexual habits I have myself investigated.

As I have recently pointed out (Huxley, '21), it is impossible in the present state of our knowledge to maintain that Darwin's original theory of sexual selection is adequate to explain the origin of most of the sexual ceremonies and adornments to be found in monogamous birds. These adornments are chiefly used in ceremonies which take place *after* mating-up has taken place for the season. There cannot therefore be a direct selection as between one male and another in respect to them. It may be mentioned

in passing that there is evidence of this direct competition (using the word in a metaphorical sense) between males in at any rate some polygamous species, *e. g.* the Blackcock (Selous, '09). What, then, is the function of the sexual adornments and ceremonies—for the most casual observation is enough to convince anybody that they possess *some* function?

It is to be observed that sexual ceremonies and colours or structures which are displayed solely or chiefly during such ceremonies are only to be found in animals of a certain grade of nervous organization. Observation on newts, which are remarkable in that the males deposit their sperm in the form of spermatophores first and afterwards go through their display ceremonies, indicates that the function of the display is a stimulative one, designed to stimulate the female to pick up the spermatophore (quoted in Pycraft, '13). The experimental work of Sturtevant ('15) on *Drosophila* entirely corroborates this view. The male in this species performs special actions with his wings when "courting" the female. Sturtevant found that males with the wings cut off, when imprisoned singly with females, succeeded in copulating, but after a longer time than normal males in a similar situation. On the other hand, when each female was placed with two males, one normal, the other with amputated wings, it was found that the wingless males were successful in copulating almost as often as were the normals. This can only be interpreted to mean that the wing-waving ceremony stimulates the female in such a way that she is then ready to receive *any* male in copulation. Morgan ('19) appears to adopt this attitude in viewing the whole sexual selection problem, but his statements are not very definite, and he does not bring first-hand observation to bear on the question.

Observation of most of the post-mating courtship ceremonies of birds bears out this interpretation. If we for a moment confine ourselves to a consideration of birds with distinct sexual dimorphism, either of colour and structure, or at least of behaviour, we can say (1) that the female is always or usually at a lower level of sexual emotion than the male; (2) that the nervous organization of birds is so advanced that behaviour is no longer merely reflex, but that it depends in the main on highly-developed instincts, each associated with a particular emotional tone. The centres for the instinct require to be stimulated before the impulse to the particular instinctive action is felt; there is a certain minimum intensity of stimulation necessary, which, as we have just said, is, in the case of the sexual instinct, generally higher in the female than in the male; (3) that, accordingly, a necessary preliminary to coition is the raising of the emotional state of the female to the level at which her sexual instinct is stimulated to action.

If we like to sum it up from a slightly different angle, we can say that in birds (as well as in other groups), mental organization has reached a pitch at which the higher centres concerned with emotion play a predominant part in

determining behaviour, and that a stimulation of the emotional centres is a necessary preliminary to coition. In a precisely similar way, at an earlier stage of evolution, a stage of general bodily organization was reached at which internal fertilization was desirable or necessary. On this stage being reached, it became imperative that coition should occur, and that, in practically all cases (the majority of birds constitute an exception), specialized copulatory organs differing in the two sexes should be developed. Both (*a*) copulatory organs and (*b*) most of the courtship ceremonies and epigamic structures we have been considering can therefore be classed under the same head—viz. as accessory sexual organs. I have heard this point epigrammatically summed up in discussion by the remark that this type of male courtship is a “psychological penis.” In any event, it is clear that just as no one has ever considered it necessary to postulate a *special type* of selection to account for the origin of copulatory organs, so the origin of courtship, so far as it is of this stimulative type, does not demand the special evolutionary mechanism of Darwinian sexual selection to explain it.

The question may now be raised as to the relationship between this “stimulative” courtship in species with sexual dimorphism and courtship in species where the appearance and behaviour of the sexes are similar. To answer this we must go back for a moment and ask a more fundamental question:—What is the reason, in the dimorphic species, for the difference in sexual excitability between male and female? There may be some primary difference between the sexes which tends in this direction, but there can be little doubt that the marked accentuation of this, which is seen in most dimorphic species among the higher animals, has for one main function, as has been several times suggested (*e. g.* especially by Groos, '98, and E. Howard, '07-'14), the *regulation of coition*. If both sexes were highly excitable, coition would occur too often; on the other hand, it would be undesirable to reduce the strength of the impulse too far, until it was near the lower level at which it ran the risk of being extinguished under the pressure of accidental unfavourable circumstances. (There is much evidence to show that, *e. g.*, cold and damp have a markedly depressing influence on the sexual activity of birds.) An obvious method of ensuring the golden mean between the danger of excess and that of possible suppression of the instinct is to have one sex with a very strong instinct, or at least one which is readily excitable, while that of the other requires considerable stimulation to arouse it. (We have already seen that the instinct must be aroused through stimulation of the higher centres.)

There is, however, another method of ensuring a similar result, and that is to have the sexes at the same general level of excitability, the male less excitable than in dimorphic forms, the female more so. In this case both sexes will constantly be reaching the level of stimulation at which desire for coition occurs. On the other hand, here again it is unlikely that both will at the same moment spontaneously reach this level—unless both were

keyed so high that an undue amount of coition resulted. Further, when the level of readiness to pair is reached, it does not follow that the bird will be under that amount of emotional tension which results in some physical expression being necessary: in fact, this appears to be the accompaniment of a definitely higher level of excitement. "Courtship" ceremonies which result in these circumstances may therefore have one of two functions. In the first place, they may be performed by one alone; they may then convey to the other that the first is ready to pair—in other words be *informative* in function—or in addition be *stimulative*, and help to key the other up to the requisite pitch. The stretching-out in the passive pairing attitude which occurs on open water in Crested Grebes (Huxley, '14) and on the nest in Dabchicks (Selous, '15) appears to be primarily such an informative symbol, although it is at least probable that it is also stimulative. On the other hand, there are many other courtship actions, such as the majority at least of the mutual post-mating ceremonies described both for the Diver and the Grebe, which appear to be primarily, or in any case, primitively stimulative in function. They are not symbolic, in the sense that they are not representations of coition attitudes, and both birds take part in them, usually though not always performing similar rôles. These have as their original function the raising of the level of sexual emotion—only here it is a mutual raising of an originally similar level. It is true that, as in the Grebe, these ceremonies are frequently what I have called self-exhausting, and do not lead to coition, but this is probably secondary; it is also probable that they may have other functions besides that of stimulating to coition. Both these points, however, we must discuss later, as also the reason for the existence of the two different methods of dimorphic and of mutual courtship.

It is no doubt often difficult to distinguish between the two; but in the Crested Grebe at least there appears to be a real distinction. Objectively ("behaviouristically"), *e. g.* the pairing-attitude is adopted only near the nest or pairing-platform, and is almost always followed closely by coition; it is not accompanied by any of the usual signs of violent nervous activity, nor by anything that can be called display. *Per contra*, the mutual ceremonies may take place anywhere, may or may not be followed by coition, and, if so, generally after some interval; they are associated with various signs of general nervous activity, and *do* serve to display special structures and colours.

Psychologically, it would appear that the coition-attitude is narrowly and specifically associated with coition, and is "informative," denoting readiness to perform the act itself; while the mutual display ceremonies are not associated with coition in particular, but with general emotional excitement. In so far, therefore, as they have a stimulative function, it is concerned with raising the general emotional level to the pitch required to make the birds repair to the neighbourhood of the nest—*i. e.* to bringing about the general

psycho-neural state *within which* the particular state of readiness to perform the act of coition itself can only occur.

In so far as they are truly self-exhausting, and not stimulative, they must either be considered as biologically functionless, as so many by-products of a mental organization of the type required to execute the stimulative forms of display (*cf.* the way in which song has in many cases become a biologically useless outlet for very various emotional states, as well as subserving its primary functions in connection with territory); or, as I have previously suggested (Huxley, '14), their function must be concerned with keeping the pair, in species in which both sexes share the duties of incubation and care of young, more closely attached to each other throughout the season.

Here we must be content to note that both types are "accessory" sexual characters, in the sense that their main function, like that of copulatory organs, is to facilitate the union of the gametes, and that they represent different methods of arriving at the same result—viz., the raising of the emotional level of the pair to a point at which coition will take place.

It may be suggested that to speak of excessive coition, as I have done, is to use a phrase which it is difficult to justify biologically. It should be remembered, however, that experiment has shown that, in mammals at least, a male will, if females in the right condition are provided, continue to pair until his seminal fluid contains very few spermatozoa (Hays, '18; Lloyd-Jones & Hay, '18). Normally, of course, this is prevented in mammals by the fact that the females only attain the condition in which they are ready for coition for very short periods at a time. A further disadvantage would accrue from the absorption of attention in the sexual act which is so marked a feature in most animals. The more frequent this might be, the more the species would be exposed to the attacks of enemies. The whole subject has been fully dealt with by Groos in his interesting book '*Die Spiele der Tiere*' ('98); and see also Mottram ('14).

The regulation of coition, however, is undoubtedly not the only factor of importance in the evolution of courtship. Previous workers on the subject have been too exclusively preoccupied with the epigamic significance of courtship. This was natural; but they should have remembered that the organism is a whole. We find as a matter of fact that the form and extent of courtship, nay, in some periods its very existence, is due to causes which are not epigamic in origin, but connected with other fundamental biological needs in relation with the annual cycle of the animal.

In many birds, as we shall find (see Howard, '20), it is of prime importance for the welfare of the pair and its offspring that a well-defined territory shall be occupied in which the nest is afterwards built, and from whose produce the young are usually fed. It is a biological advantage to occupy territory early; birds which did not do so until late would find all available space taken up, and would have to fight for occupation. When the sexes are dimorphic, one will usually be the more active in this task—almost invariably



the male. But once he has occupied the territory, it will be again a biological disadvantage for the female to put off too long her quest for territory-plus-mate, or else she too will find herself forestalled.

On the other hand, the exigencies of the food-supply demand that oviposition should not occur until a certain date, varying naturally for different species, but almost always considerably later than the date at which territory is occupied. Thus we have two opposed advantages—one in the early occupation of territory, one in the late starting of coition. As a result, there will be a period after both birds are on the territory—*i.e.* after pairing-up has occurred—when it will be biologically undesirable that oviposition should occur. This we may call, if we choose to adopt a not wholly suitable human metaphor, the “engagement period.” Extremely little is known concerning this period in species with mutual courtship: in many of them it is absent, the birds only returning to the breeding-grounds, or only pairing up, immediately before coition can and does occur. (This is apparently the case in Snowy Egret, Louisiana Heron, and many cliff-breeding birds.) In any case, what is known is so slight as to make discussion unprofitable.

In many dimorphic species, on the other hand, a good deal is known. Such an “engagement period” occurs apparently in all small *Passeres* which have nidicolous and insectivorous young, and which therefore, as Howard has demonstrated, imperatively require a territory which is not merely a nesting-area, but a hunting-ground from which the needs of the new-hatched young may be supplied. As we shall see later, the dimorphism itself has probably been evolved in relation to other biological needs of the species—*viz.* the necessity for concealing coloration and behaviour in the female. Here, however, we shall take the dimorphism as given.

The simplest way of satisfying these biological requirements is to make the male enter in early spring on to a sexually-excited state in which he is impelled to seek and occupy territory, to pair or attempt to pair with any female who stays in the territory, to assist in feeding young when hatched, etc. So far as his endocrine excitation goes, he remains in the same phase throughout the season.

With the female, however, the case is different. She must pass through at least two phases of excitation—the first sufficient to impel her to abandon the “neutral” non-sexual existence of the winter and to seek and if necessary fight for (Pl. 15. fig. 7) the company of a particular male, but not sufficient for coition to take place; the second, more intense, impelling to coition and nest-building; when the eggs are laid, to incubation; and, later still, to the care of the young.

There will thus exist a period in which the male will be anxious for coition, but the female will not permit it. Further, the biological causes for the existence of such a period are not epigamic, not concerned with the relation of the sexes, but are to be sought in relation to the need for occupying

territory and the need for nesting at the proper time for supplying the food-requirements of the young.

Such species, where territory is of major not of merely minor importance (*feeding territory* as opposed to merely *nesting territory*), we may for convenience call "territory birds." In them, during the female's second phase, there is comparatively little "courtship" on the part of the male. When the female feels impelled to coition, she adopts a particular attitude, and the male immediately performs the act. The bulk of the "courtship" (excluding song) is due to the fact of the existence of the "engagement" period when the male and female are in different states of endocrine excitation, and this is a biological "accident" arising as a by-product of other needs and functions.

The song, on the other hand, is, in territory birds (where it reaches by far its highest development), connected primarily with territory—with attracting females to, and warning other males off, occupied areas. The displays and pursuit flights are merely an expression of the desire of the male for coition, a desire which cannot be satisfied in the engagement period. The display is in origin an adoption of the coition attitude itself, or something closely resembling it, brought about naturally as a result of brain-structure when a certain level of sexual excitement is reached; the pursuit flight is in origin an attempt to force the female to submit to coition.

Once, however, these actions had arisen in this way, they formed a possible basis for further evolution. The fact that in large numbers of species of this type the male is brightly coloured, and brightly coloured in such a way as to display the bright colours in the above-mentioned type of ceremony, is evidence, though of a merely circumstantial kind, that something of the sort has occurred, and that the ceremonies, originally mere attempts at coition, have later acquired a second and presumably stimulative function. The fact that the males of some territory birds are not brighter than the females (*e.g.* the Warblers) may well be accounted for on the supposition that in these species protection is desirable for both sexes.

There is, further, interesting evidence to show that these ceremonies probably do possess some stimulative function.

I am informed by Mr. Howard—and the statement has been in general corroborated to me by Mr. Jourdain and other field ornithologists—that in seasons when the weather has been very cold and unpropitious during the time of egg-laying and immediately before, the average number of eggs in a clutch is smaller than usual, and that the proportion of infertile eggs is higher than usual. This latter effect may in part be due to actual damage to fertilized eggs soon after laying, caused by the inclement conditions; it may also be due to failure of fertilization. The smaller number of eggs in a clutch must be due to failures in ovulation. It is further well known that ovulation in birds is, in part at least, under nervous control; the caressing of a female virgin dove on the back of the neck with the hand causes ovulation.

Harper's observations (discussed by Marshall, '22, pp. 134-135) make it clear that the female pigeon will not ovulate unless stimulated emotionally. This stimulus is normally provided by the male; but two females isolated together will often lay. Single females when isolated never lay (except occasionally when overfed, and then only a few eggs). The recent work of Chance ('22) indicates that in the common Cuckoo ovulation occurs under nervous control, the sight of a pair of foster-parents building their nest acting as a stimulus. It is obvious, further, that the willingness of female birds for coition is not almost exclusively a matter of internal secretion as in mammals, but is largely under emotional control. It is also well known to field observers that the state of the weather has a marked effect upon the emotions and their expression in birds; song and display is regularly far poorer on a cold, dull day than on a bright, warm one. Other things being equal, therefore, anything which tends to counteract the depressing effect of bad-weather conditions upon the emotions and the actions under their control will be of biological advantage in that the number of ovulations will be increased, and also the number of coitions, and so the chances of fertilization for the eggs after ovulation. There would thus in ordinary seasons be no marked biological advantage gained from stimulative ceremonies; this would accrue in exceptionally bad seasons only.

It appears, as I have already indicated, that in birds with mutual courtship the ceremonies do have a stimulative effect, although this is usually of a general and indirect kind, keeping the level of sexual emotion up to a constant pitch, and occasionally heightening it so that visits are made to the pairing-platform, &c., where coition will usually occur. It is highly probable that a similar general stimulation is exerted by the more primitive displays of the "territory" birds, although here the stimulation is not mutual but unilateral.

It is further clear that any display which did have such an effect would reap the biological advantages, mentioned in the preceding paragraph, of counteracting the bad effects of cold seasons. As a matter of fact, even in these bad seasons some nests will be found with full clutches of eggs and normal proportion of fertile eggs. There is, therefore, a form of natural selection actually in progress here, which (as often) is only operative in particularly adverse conditions.

It is of very great importance that this point should be cleared up, and that field ornithologists should undertake careful statistical work on the relation between weather, number of eggs in a clutch, and percentage of infertility. It is only so that firm bases can be found for biological theories.

It must now be asked, as regards stimulative displays, what form of stimulus has been adopted and why. So far as males of dimorphic species are concerned, what is the position? It is that they are subjected to a mental state which is comparatively rare in organisms below man, of being stimulated by a powerful emotion but being unable, so long as the female

remains passive, to express it physically by the natural channel proper to the instinct which it accompanies. What will the consequence be? It will be that the psycho-physical energy will discharge into other motor channels, since it is debarred from discharging into its proper and normal channels.

Perhaps the most frequent way in which it is discharged in birds is by rapid, restless movement, accompanied by drooping and partial spreading of the wings, spreading of the tail, and erection of feathers, especially on the head and breast. This type of action seems to have had a dual origin. In the first place, it is often very similar to the actions normally adopted at coition, *e. g.*, as Mr. Howard informs me, in the Buntings. In the Warblers the similarity is still marked, but to a lesser degree. As I have suggested, it is probably the direct result of the unsatisfied desire for coition. In the second place, however, it appears to represent the result of a general state of excitement, quite apart from any representation of coition attitudes. It is often difficult in any particular courtship ceremony to disentangle the share of the two contributions. In the Grebe, for instance, the ordinary ceremonies are in no way representations of coition actions, while in the Buntings they are almost wholly so. In any event, the dual origin of the ceremonies as a whole is clear—general expression of hyper-excitation combined with more or less of the typical coition attitudes.

Once this type of action exists, however—and it will inevitably come into being in some form or other in the conditions which we have outlined,—it will naturally form the chief basis for the development of specialized courtship actions and courtship colours and structures belonging to the stimulative type. When it is the wings and tail which are spread and the crown and breast-feathers which are erected, it will be inevitable that, if further stimulation is advantageous, it will in the main be achieved by making these parts more conspicuous (so as to accentuate the difference between the normal appearance of the bird and its appearance under the influence of sexual emotion); and this will be most readily done by the development of bright colours on these parts, or by the formation of special structures in these regions—structures which are usually displayed in full only under the influence of sexual emotion. Since the form of the wings cannot be much altered without interfering with the efficiency of flight, it follows that special courtship structures will not often be developed in connection with them; and as a matter of fact we find that the chief special courtship structures are crests on the crown (as in Peacock, Herons, Goldcrest, Pewit, Cranes, &c.) or breast-plumes or other structures on the breast (as in Herons and Egrets, Bustard, Umbrella-bird, &c.), or elongations or other specializations of the tail (*e. g.* Pheasants, Humming-birds, Blackcock, Lyre-birds, &c.) or of the tail-region (Peacock, &c.).

The erection of feathers on other parts than crown or breast is also common, and its specialization gives us structures like the ruff of the Crested Grebe and that of the Ruff, the elongated scapulars of Herons, and those, both

elongated and dissected, of Egrets, together with some of the peculiarly situated plumes of Humming-birds and Birds-of-Paradise.

It appears, then, that "courtship" consisted at first chiefly of non-significant movements employed by the male as an outlet for the pent-up sexual emotion, these being in part derived from those employed in coition, and that special colours and structures displayed only mainly during these movements are later specializations. If so, then we should expect to find some species of birds in which the movements exist, but not the special colours or structures—"courtship" actions without epigamic colours or structures. This is as a matter of fact the case. The Sylviidæ, for instance, give us many examples of species which are not dimorphic in colour, or only so to an obviously non-significant extent, but are dimorphic in behaviour, usually the males alone performing special post-mating ceremonies, apparently stimulative in function, in which wings, tail, and feathers are moved in the general way that has been described (E. Howard, '20). Rarely, however, both birds perform ceremonies simultaneously, as is shown in fig. 8 (Pl. 15). But the two perform ordinary unilateral ceremonies, and not in any common rhythm. There is no sign of a unified mutual ceremony. It is an interesting intermediate type of behaviour.

Usually, however, the close observation of the courtship of a species reveals other behaviour which cannot be brought under the rubric of originally non-significant physical release of emotional tension. I refer to actions which are to be thought of as having originally been developed in connection with certain other functions, and later having been connected with sex in courtship displays. Such actions have already been referred to. Sometimes they are to a certain extent associated with sexual emotion, as are all those connected with nesting-material; sometimes they appear to have no such connection, such as the preening, head-shaking, dipping of the bill, &c., which we have noticed in Divers and Grebes. In Mute Swans, I recently observed some interesting courtship-actions, and there one of the prominent pieces of behaviour was the dipping of the whole head and fore-part of the body below the water; the action was strongly reminiscent of an incipient attempt at reaching down to feed in the characteristic swan manner. The birds also repeatedly preened themselves in a manner very similar to that seen in the Grebes—*i. e.* a manner indicative of the action being used in what I may call a ritual way, and without any of its usual functional significance. I am confident that when once attention has been drawn to this "ritual" use of non-sexual actions during courtship activities, it will be found to be of very wide occurrence. Prof. H. Balfour informs me that it occurs commonly in the Gannet. The association of nesting-material with courtship is certainly very widespread, and here we may probably see the working of direct association. The sexual emotion directly activates the centres connected with nest-building and the handling

of nest-material, because the two activities have been so often actually connected. But we cannot adopt this comparatively simple explanation for the incorporation of wholly non-sexual activities, such as preening, in courtship. So far as my personal experience goes (and so little attention has been devoted to the matter that the literature is of scarcely any help), the birds which make most use of these non-sexual actions in courtship are those which make least use of the peculiar expressional movements of wings, tail, and feathers generally, which we saw made up the raw material of courtship actions in most species. If this should turn out to be generally true, then we should have to suppose that the emotional tension, since for some reason it does not in these birds express itself in the originally non-significant methods of general wing, tail, and feather movements, must find an outlet elsewhere, in the guise of actions which are already performed by the species in other connections. In any case, it is clear that these actions are utilized, like the general non-significant actions, as physical relief or expression for emotional tension; and that since they are already given in the bird's instincts and habits, they form the natural raw material—the natural outlet for surplus psycho-neural excitement due to emotion temporarily unable to find its normal expression.

In a sense, therefore, the non-sexual associated actions are mere expressions of emotion, comparable to the meaningless acts often performed by men under the influence of great emotional tension. But once they have come to be associated with sexual emotion, they then become the raw material which can be worked up into more elaborate courtship ceremonies. Such, for instance, appears to be the origin of the head-shaking ceremonies in the Crested Grebe. In diving birds generally, there is an almost universal habit of shaking the head on emerging after a dive. This is, as we have seen, slightly associated with sexual emotion in the Diver, but in the Grebe the head-shaking is a very elaborate part of highly-specialized ceremonies, and its origin from ordinary non-sexual head-shaking can only be deduced from indirect evidence. Unless, however, its origin be of this nature, it remains quite obscure.

The association of diving with courtship in both Grebe and Diver may be adduced as further proof of our contention. The special "splash-dives" in the Diver, and the emergence from the water in a vertical attitude which occurs in both species, are both obviously modifications of the ordinary diving practised for food, which have now an exclusively emotional significance, and a sexual function. Under the influence of unsatisfied sexual emotion the bird indulges in various forms of action habitual with it; later, specialization has taken place so that the sexual modes of diving become quite different in appearance from the original non-sexual mode.

As a matter of fact, when we survey the varieties of courtship, we find that they are not uncommonly to be regarded as specializations of normal

activities of the species. For instance, various hawks (*e. g.* Kestrel and Peregrine) have courtships which are based upon the wonderful powers of flight possessed by the group; while many water-birds, like Grebes and Divers, show courtships in which some normal aquatic performance is sexually utilized. Thus in considering the genesis of courtship ceremonies, we have to distinguish between the raw materials and the later specialization. The raw materials are (1) coition-attitudes; (2) originally non-significant general movements, especially of feathers, wings, and tail; (3) actions originally connected with activities in themselves associated with sexual emotion, such as nest-building; (4) actions originally subservient to some non-sexual function.

Later, specialization consists (1) in the development of striking colour on parts prominently displayed in the raw actions; (2) in the development of such parts to form special structures (*e. g.* tail-coverts of Peacock, ruff of Crested Grebe).

The difficult question remains as to the reasons for the existence of dimorphism of courtship in some species, but of mutual ceremonies—associated, be it remembered, in the majority of species, with special colours and structures of as definitely sexual (epigamic) significance as in dimorphic forms—in others.

In general, it appears that it must have some connection with mode of life, although in the absence of detailed information on many birds, and of statistical treatment, our conclusion cannot be wholly satisfactory at present. In the first place, it is undoubted that polygamous species present the most extreme cases of male adornment, combined with protective colouring in the females. Secondly, in monogamous species with marked male adornment, the females are usually protectively coloured, and usually undertake the whole of the duties of incubation—*e. g.* Anatidæ, such of the Pheasants as are monogamous, &c. In some forms with dimorphic courtship, such as the Sylviidæ, the two sexes are often not very distinct, and are both more or less protectively coloured; both sexes may incubate here, although the female does so much more than the male. The Sylviidæ may be regarded as primitive in respect of the evolution of post-mating courtship. The Fringillidæ are, on the whole, somewhat similar to the Sylviidæ, save that the colour-dimorphism is usually more marked and the male usually incubates less. E. Howard ('20) has recently shown that territory plays a great part in the lives of birds, and that, in both Sylviidæ and Fringillidæ, it is the male who, early in the season, before other manifestations of sexual emotion, occupies a definite territory. Singing then begins, and is associated with the possession of territory. The process of mating-up consists mainly in the disputes of females for occupied territories with their contained males (Pl. 15. fig. 7). Since the whole breeding-life of the birds is connected with the staking-out of territory at the earliest possible opportunity by the males, it follows that

these must possess different instincts from the females—instincts which begin to react to seasonal influences some time before any reaction occurs in the other sex. Here we have a primary basis for the rest of the dimorphism observed—a basis given by territory requirements, not by epigamic needs.

In birds with both sexes similar in appearance and with mutual courtship, two salient facts are to be noted. In the first place, the birds are usually not protectively coloured, or at least not to such an extent as in most dimorphic species. Take for example the Herons and Egrets, the Swans, the Gulls, and many of the cliff-dwelling and other sea-birds (Guillemots, Razorbills, Petrels, &c.). The Grebes and Divers are intermediate—the main coloration is protective, but the head, neck, and under-surface are conspicuous and used in courtship. In the second place, both sexes almost always share in nest-building, and often in incubation and the care of the young. So far as I know, there are no birds with mutual courtship in which the males do not share some of the duties of parenthood, and their share is on the average certainly greater than is that of the males of birds with dimorphism in courtship. Also the nest-site is, usually at least, chosen by both birds jointly.

It appears to be definitely the case that several tendencies are at work to produce the variation in modes of courtship that we see. (1) Where, as in the Warblers, &c., the whole life-cycle is based on the early staking-out of territory by the males, there must be a dimorphism of instinct in connection with this, and this primary dimorphism tends to be continued in other ways, *e. g.* courtship. (2) Where protective coloration is of great importance to a species, it is imperative that one sex at least shall be thus protected: this sex will naturally, save in very exceptional cases, tend to be the female. If protective coloration is desirable, it will almost always follow that general inconspicuousness will be desirable; this will mean that any violent manifestations of emotion, whether in the form of song or of display, will be undesirable. Hence there will be a tendency in such species to depress the level of sexual excitability in the females. This in its turn will, however, make it necessary for there to exist some mechanism for arousing their sexual emotion, and this will naturally be found in the courtship of the male. Thus in general the necessity for inconspicuousness in the female will have as natural reaction a tendency for courtship activities to be confined to the male, and to be well developed in him. Inconspicuous females tend to be associated with dimorphism of courtship, and often of colour. The tendencies mentioned in (1) and (2) often interact so that it is hard to distinguish which is the primary. Where polygamy prevails, and the males take no share in parental duties, this tendency will naturally produce its most marked results. (3) In some groups, such as for instance the Herons, not only is it necessary for both birds to share in feeding the young, but also to share the duties of incubation (since the feeding-



grounds are so distant; furthermore, protective coloration, as in most colony-breeding birds, is unnecessary. Here we find two tendencies acting in the direction of similarity in appearance and behaviour. In the first place, there is no need for the female to be inconspicuous, whether in plumage, voice, or action; thus, *ceteris paribus*, there will be no tendency to restrict any variations in the direction of greater conspicuousness—even if they may have been first acquired by the male sex, which is by no means necessary—to the males. Secondly, since the male as well as the female must possess the instinct to incubate and to feed the young, it follows that there is a tendency to approximate the instincts of the two sexes in these particulars; and the sex-similarity thus initiated again tends to be continued in other ways, unless there are reasons to the contrary, which, in birds to whom inconspicuousness is a matter of indifference, we have just seen do not exist. In birds of this type, therefore, there exist again two mutually reinforcing tendencies which tend to bring about a similarity of plumage and instincts, and so lead to mutual courtship.

There are, it is true, species like certain Penguins (Levick, '14) in which the sexes are alike, but much of the courtship is not mutual; there are other species, like our Red-throated Diver, in which the sexes are similar and there exists mutual courtship, but in which the male helps to a comparatively small extent in incubation. In such a complicated subject we should not expect to find universal hard-and-fast rules; each case requires to be investigated on its merits, and with a thoroughness which has so far only characterised few workers. But that the two general tendencies which I have mentioned, to dimorphism and to mutualism, do exist, and that they are definitely correlated with other characteristics of the species' life-history in the general way I have sketched, appears to be incontestable.

One other point remains to be considered here. Why is it that among birds with mutual courtship, some, like Divers and Grebes, perform ceremonies far from the nest, no emotional expression being seen at or close to the nest during incubation and the care of the young, whereas in others, such as Herons, Egrets, Pelicans, &c., the chief ceremonies observed are those which take place at the nest or nest-site, especially at the moment when one bird relieves the other from the duty of incubation? (Pl. 14. figs. 5 & 6).

The answer is not, I think, far to seek. The "nest-relief birds," as we may call the latter category, are all species in which the nest is not concealed, and does not appear to be in need of special protection against enemies. In most cases the birds nest in colonies. The birds with mutual ceremonies which are unconnected with nest-relief, on the other hand, have nests which are carefully concealed, or at least are far from conspicuous, and rarely breed in colonies.

When a sitting bird is rejoined by its mate, especially if the mate's presence implies a speedy relief from the tedious business of incubation,

it is natural that emotion should be aroused. If there is no biological reason against the expression of the emotion, it will naturally be expressed then and there in some form of ceremony. On the other hand, if there are biological reasons for concealing the position of the nest from enemies, then it will be desirable not to draw attention to the spot by conspicuous sounds and actions, and selection will see to it that the emotion is not expressed immediately and naturally at the nest, but at a distance from it. The fact that, in the Crested Grebe, there exists a special and very elaborate ceremony which occurs when the members of the pair rejoin each other after having been separated for some time, indicates that in this species too the same emotions occur in similar circumstances, but are not allowed expression in the neighbourhood of the nest.

Here again, therefore, we find an influence of the general mode of life upon the form of the courtship. So that we may really say that, although, given in the first place the state of general excitement produced by the sexual hormones, in the second place the stimulative effect of sexual display, and thirdly the necessity for regulating coition, there will inevitably come into being displays, &c., which go by the general name of courtship, yet the *form* of the courtship, not merely in details but in broad lines as well, will depend in the main upon other general biological factors affecting the species.

There remains to be considered the physiological and genetic mechanism which we must suppose responsible for the phenomena; but before passing to this, I should like to summarize briefly the conclusions just reached. In few words they are these:—

1. Polygamy encourages sexual dimorphism. It is only found among birds with nidifugous young, since nidicolous young require that both parents should assist in feeding.

2. Need for inconspicuousness encourages dimorphism.

3. Nidifugous habit in the young facilitates the development of dimorphism otherwise initiated.

4. Early occupation of territory by one sex encourages dimorphism.

5. Absence of need for inconspicuousness encourages mutualism.

6. Need for incubation by both parents encourages mutualism.

In addition, there are no doubt many special physiological points which encourage one or the other tendency; but in general the condition observed is the result of the interaction of the tendencies we have enumerated.

Recent experimental work is beginning to give us an insight, albeit but a partial one as yet, into the physiological and genetical mechanism underlying sex-characters in birds.

It appears that castration of a male, in highly dimorphic species like fowl and wild duck, produces birds which are neutral in instincts but remain male in plumage.

In females, on the other hand, castration produces cock-feathering, but not male instincts.

Recently investigations have been made on breeds of fowls like the Sebright Bantams, in which the cock is hen-feathered. Two interesting points have emerged. The first is that the condition is due genetically to a Mendelian gene, the second that it is due physiologically to the fact that the male gonad in these animals possesses the same substance as do the gonads of normal females, which inhibits the development of male plumage. This latter point is demonstrated by castrating hen-feathered cocks, upon which they become cock-feathered—a strange but conclusive result (Morgan, '19). Morgan believes that the condition has its histological basis in the development of luteal cells in the testes of hen-feathered cocks, similar to those found in the ovaries of normal hens, but recently Pease ('19; *q. v.* for references to previous work) has thrown doubt on this.

In any case, the facts are of great interest as showing by how simple a means, and in how few generations, a dimorphism of plumage could be converted into a similarity. On the other hand, it also shows that in this dimorphic species at least, plumage and instincts (as the castration experiments also demonstrate) depend upon different mechanisms for their development. The development of male or female instincts is due to a positive effect exerted by some secretion of the male or female gonads respectively, acting upon a basis which is neutral in the absence of the specific secretion, whereas the male gonad has no positive effect upon plumage development (the plumage of capons being, if anything, more male than normal), while the female gonad exerts in this respect an entirely inhibitory effect.

It must be emphasized, however, that we have no experimental information with regard to species with similar plumage and courtship (in passing, it may be remarked that the castration of Grebes or Herons should provide interesting results). Further, from the general considerations advanced above, it is clear that we should not expect precisely the same mechanism to hold good in "mutual" as in dimorphic species. In the latter, as we have seen, selection must have been at work emphasizing and exaggerating any sexual differences of instinct which primitively existed; whereas in the former all the influence would tend in the other direction, of assimilating instinct in the two sexes.

To what pitch this has as a matter of fact been carried is shown by the observations of Selous and myself upon the Crested and the Little Grebe (Dabchick). The Grebes are birds in which mutual courtship attains the highest development yet described, and in which sexual adornments similar in the two sexes attain a great specialization. In the two species mentioned, and probably in others, the instincts of the sexes are so alike that coition occurs both in the normal or in the reversed position. In these birds, coition always takes place upon a nest; the "passive" bird extends itself at full length in a perfectly horizontal position, the "active" bird mounts the other from behind, and, after coition, walks up its body and off by its shoulder.

The differentiation of action between the sexes is thus very considerable ; yet in spite of this, as I say, either sex adopts either position according to circumstances. In the Moorhen, Selous ('02) has described reversed pairing as a normal sequence of pairing in the usual position. Mr. E. Howard tells me that he has repeatedly had occasion to confirm this himself. In Doves and Pigeons it may also occur (Whitman & Riddle, '19 ; Marshall, '22, p. 690).

It should be remembered that sexual dimorphism to any marked extent is a late development in most groups. Primary and accessory organs are, naturally, different, but general coloration and body-form is usually similar in both sexes in primitive animals—*e. g.* Echinoderms, many primitive insects ; Crustacea and other Arthropoda, Cyclostomes and most fish. In any case, recent work has made it abundantly clear that the genes for the secondary sexual characters of both sexes are normally carried in all members of the species, and that either the sex-chromosome mechanism ensures two quite different types of cellular metabolism, one permitting the development of male, the other of female characters, as seems to be the case in insects, or else that special hormones are developed in the gonads which exert specific growth-promoting effects upon some sexual characters, inhibiting effects upon others, as in vertebrates (summaries in Marshall, '22, ch. 15 ; Goldschmidt, '20 ; Huxley, '22 a).

If, therefore, the divergence which I have referred to between the sexually dimorphic and mutualist types of birds originated early, as it seems to have done (for the distinction characterizes whole groups of the class), we may suppose that the primitive bird species on which it acted were probably similar in appearance, without well-marked courtship colours or structures, whether in one or in both sexes, and with a moderate dimorphism of instincts. Later development has either accentuated the difference of instincts, as in the Sylviidae, or the divergence of instincts and of appearance, as in most Gallinaceous birds ; or has allowed bright colours to develop, apparently for use in courtship, but has not confined them to one sex, although it has not closely approximated the instincts of the two sexes (as in the Penguins, Levick, *loc. cit.*), or finally has encouraged sexual adornments similar in the two sexes, together with markedly mutual courtship, and has approximated instincts to a high degree—as in the Grebes.

So far as observation can be a guide in these matters, it appears that although sex-dimorphism in plumage may depend upon different genetic and physiological factors from that in instincts and from that in size, yet as a matter of evolutionary fact, the first two, and probably the third also, have gone hand in hand.

In other words, the divergence between dimorphic and mutualist species is primarily dependent on whether the gonadal hormones remain as similar as is compatible with primary sex-differentiation, or whether they become considerably different in the two sexes. If they adopt this latter alternative,

then there will result, unless special circumstances arise, a simultaneous dimorphism in both appearance and instincts ; if they remain on the whole similar, there will be (again unless there are special reasons against it) a similarity between the sexes, not only as regards appearance, but also as regards courtship and parental behaviour.

If this turns out to be well founded, and the gonads do normally in birds determine appearance, behaviour, and size simultaneously, then it is clear that observation will have contributed important guiding lines for future genetic and evolutionary research.

In conclusion, I would like to emphasize the fact that, even when both sexes are similar, there is often no doubt whatever that the coloration and special structures used by them both in courtship have been evolved in relation to sexual habits, and in essentially the same way as bright colours and special structures used in courtship by males alone in dimorphic species. They have arisen through the necessity of providing an emotional stimulus to the other member of the pair, if fertilization is to be normally and easily effected, particularly in the face of adverse environmental conditions ; and from the reverse point of view, have become necessary because it is biologically desirable to keep the mean sexual excitability of the pair at a level low enough to prevent excessive coition. They are, to use the useful term of Poulton's which I have for some time adopted, always *epigamic*, although not always *secondary sexual* characters. They have also been usually grafted on to primitive ceremonies which are the direct outcome of sexual excitement, and indirectly often the result of an "engagement" period which is caused by non-sexual exigencies of the life-cycle.

Although the direct competition among males, which was one of the main points of Darwin's theory of sexual selection, does not appear to occur in the evolution of most epigamic characters among birds, yet it is noteworthy that in the polygamous species in which it *does* occur, the type of coloration and structure which is evolved is very similar to that evolved in monogamous species, except that development has usually gone to further lengths of specialization. This similarity between the end-results in what we may call "accessory" as well as in "sexually-selected" epigamic characters, is due to the second salient fact first clearly recognized by Darwin—the fact that the development of an epigamic character is dependent upon the emotional effect which it produces upon the mind of a bird of opposite sex. Epigamic characters must be emotionally stimulative if they are to perform their function successfully ; and to be emotionally stimulative, it would appear that they must be first striking, and secondly not usually visible, so as to have, when they are displayed, an element of novelty and unfamiliarity which adds to their stimulative effect. So far as their striking quality is concerned, they may be either what seems to us beautiful or else what seems to us bizarre. So far as unfamiliarity goes, it should be remembered that many epigamic

characters are special structures only fully displayed during courtship (*e. g.* scapulars of Egrets, tail-coverts of Peacock, ruff of Crested Grebe); others are special patches of colour only made prominent by special display actions (*e. g.*, white on wings of Blackcock and of Crested Grebe, red of legs of Red-shank, rich purplish-brown of neck of Louisiana Heron); while still others, although always present, are probably not prominent unless the two birds are close to each other, and in certain relative positions characteristic of courtship. This is probably the case with many of the curious patterns characterizing the *front view* of birds at short range (*e. g.* Blue Tit, Turnstone, Redstart, Ringed Plover); that this is the probable explanation is shown by the fact that when special structures with undoubted epigamic function are developed on the head, these are often displayed so as to appear most striking (or only so) when seen in this way, close up and from the front (*e. g.* the ruff and ear-tufts of the Crested Grebe, the crest of Louisiana Heron and Little Egret).

The existence of true sexual selection as found in polygamous species thus encourages the same tendencies in epigamic characters as does the selection of those with a purely "accessory" function: but, owing to the fact that in polygamous species the males take no share in incubation or the care of the young, dimorphism can proceed to its limit, and owing to the fact that there is a real selection as between different males, and so greater competition in regard to secondary sexual characters, and that the successful male transmits his qualities to a greater number of offspring, the process of evolution of epigamic characters is not only more rapid, but also is generally carried to a higher pitch than in monogamous species. In other words, polygamy and its attendant true sexual selection simply accentuate the same processes that are operative whenever epigamic characters are being evolved, even in the absence of sexual selection proper.

This development of epigamic characters in relation to the *mind* of the opposite sex is a point of very general biological interest, since it is the only example, in organisms below man, of a secondary effect of the mind of a species upon the evolution of that species. Mental qualities of course normally have survival value, but this is quite a different matter; they thus determine the survival or extinction of the species, not its modification in new ways. The mind of one species may play a part in moulding the evolutionary development of *other* species, as when acute vision on the part of predaceous animals renders concealing coloration advantageous, or the visual and olfactory preferences of flower-visiting insects are reflected in the development of colour and scent in the flowers visited. Lloyd Morgan ('21) has recently emphasized the influence of mind upon evolution by introducing the useful term "Psychical Selection." As indicated above, however, further terms are needed to distinguish between psychical selection acting upon the evolution of *other* species, as in the case of the mental qualities of bees influencing the evolution of flowers, or upon the evolution of the *same* species, as in the development

of stimulative display characters. If the barbarism be permitted, the terms "heterospecific" and "autospecific" psychical selection might be employed to make this distinction. But once epigamic characters come to be advantageous, the mind of the species (in the females in sexually dimorphic forms, in all individuals in those with mutual courtship) is exerting the indirect effect we have been describing upon the future development of colour, structure, and behaviour in the race. This is the most important fact which Darwin perceived, and this stands firmer than ever in spite of the rejection of the bulk of the other part of his doctrine.

In concluding, I should like to thank Professor Lloyd Morgan, Mr. Eliot Howard, and Mr. A. M. Carr-Saunders, all of whom have kindly read the foregoing article in manuscript, and have helped me with several important criticisms and suggestions.

New College, Oxford,  
March, 1923.

POSTSCRIPT 1.—Since the above was written, Dr. J. C. Mottram has been good enough to write to me on a number of points concerning sexual coloration in birds, and to allow me to see the MS. of an unpublished paper on the subject. I would like to take the opportunity of dealing with a few of the points which he raises in this and in his book ('14).

He points out the great importance in many birds of concealing coloration—a proposition in which every naturalist who has studied birds in the field would agree with him. I have in the body of the paper dealt with the ways in which the necessity for concealment or its absence reacts upon the "courtship" characters and activities of birds.

With reference to the Kingfisher (*Alcedo ispida*), Dr. Mottram makes out a strong case for believing that its brilliant colouring, present of course in both sexes, is aposematic, with the function of warning possible enemies of the bird's unpalatability. He points out that records of the Kingfisher being attacked by birds of prey are extremely rare; and has found that its flesh is unpalatable to man and rejected by domestic animals.

However, if the Kingfisher really, as seems probable, presented an example of warning coloration, it would in no way invalidate my general conclusions; it would merely corroborate from a new angle what I have been urging in this paper—viz., that each species of bird must be worked out on its merits, and that coloration and behaviour are always determined not by one single cause, but by several, of which the two most important are (a) the bird's relations with its mate, and (b) its relations with its enemies and its prey.

Dr. Mottram, however, goes farther. He attempts to account for *all* "courtship" characters and actions solely in terms of the bird's relations with enemies and prey.

(1) By an ingenious train of reasoning he points out that where the hen alone, or chiefly, incubates, she must be regarded as biologically the more

valuable of the pair, and that in such species the display and song of the cock has as its primary function that of drawing the attention of enemies away from the hen ; so that, if one of the two is sacrificed, it shall generally be the less "valuable" male.

(2) Where the species is capable of defence, or is unpalatable—*i. e.* does not require protective coloration—he postulates that courtship should be not elaborate, or may even be absent.

(3) Where both sexes are of equal biological value (*i. e.* where both incubate), he postulates that both should indulge equally in display.

The reasoning is undoubtedly ingenious, but can be shown not to be adequate to account for all the facts.

As regards (1), it should be remembered that the song of male "territory birds" is most powerful before any females have arrived. It could be no possible advantage to the species to have attention attracted to the males when there were no females present from whom attention could be drawn off.

It is undoubtedly true that where only the female incubates, and where protection is desirable, dimorphism of sexual characters and behaviour will be encouraged. This I have pointed out in the body of the paper. Dr. Mottram simply restates the problem from a different angle, and with the epigamic side of the matter left out.

(2) is simply not true in a number of cases. Herons and Egrets are well protected from enemies, but have an elaborate courtship. So do Swans (Selous, '13, and my own observations). So do Hawks, though here the displays are concerned with flight, not with bright coloration (Owen, '16-'22, Sparrow-Hawk ; Kestrel, my own observations) ; and other examples could be quoted.

(3) Where both sexes are of equal value, it would appear on the face of it biologically desirable that both should be rendered *inconspicuous* when concealment is in any way desirable, if, as Dr. Mottram would have us believe, the chief function of display is to attract the attention of enemies. However, in the Grebes, all of which take great pains to conceal their nest, and are protectively coloured so long as they are in the normal swimming, feeding, or resting attitudes, elaborate mutual courtship does occur, and at once makes the pair conspicuous. The same, to a less extent, is seen in Divers. The vocal duets of Owls which go on in the breeding-season (Huxley '19) are difficult to account for on any theory which relates them only with attracting the attention of enemies.

Finally, Dr. Mottram makes the point that since many birds "get on" without bright colouring in one or both sexes, and yet reproduce, therefore when bright colouring is present it cannot be supposed to have any relation to reproduction. This, however, is an old fallacy, repeatedly exposed since the early days of the evolution controversy. It would be equally justifiable to say



that because an earthworm gets on without eyes, and yet reacts to light and darkness, therefore when eyes are found, they can have no relation to light-perception ; or that because lower mammals get on with a small brain, therefore the difference in brain-size between them and man can have no relation to the functions carried out by the brain of lower mammals ; and so on, *ad lib.*

It becomes increasingly clear that to interpret the behaviour and evolution of a bird, even if apparently in only one regard, it is necessary to take into account *all* the circumstances of its life. As regards coloration and "courtship" behaviour, I hope I have shown that relation to enemies and relation to the mate are two factors of greatest importance. I am grateful to Dr. Mottram for having brought to my notice a number of points concerning the relation of birds to their enemies of which I was not aware ; and I believe that his contribution to the theory of the subject is of real value. But so long as cases remain—as they do in large numbers—where coloration, structure, or behaviour have an obvious function in regard to the opposite sex, and no discoverable function in relation to the enemies or any other factor of the bird's life, I maintain that we must take these into account, and that Dr. Mottram is definitely wrong in attempting to base his theory of the evolution of courtship solely on one, instead of on both of the two main factors mentioned above.

On the other hand, his suggestion that the bright colour and general conspicuousness of the male may have in some species the function of drawing the attention of enemies from the biologically more valuable female will, I believe, prove of importance in certain puzzling cases. I will mention but two. In the first place we have the well-known fact that many mimetic species of butterflies, including some of the most striking examples of mimicry (e. g. *Papilio dardanus*), are mimetic in the female sex alone, the male being conspicuous but non-mimetic. The males are "valuable" only before copulation : the females until after oviposition, and further, have usually a poorer flight. If a certain average toll is taken of the species by enemies, it could well be a real advantage to have it fall preponderatingly on the male sex.

The second example concerns birds. Reflection will show that the bright colours of male birds fall broadly into two categories—those which, like the "tail" of the Peacock or Argus Pheasant, are only conspicuous in display, and those which, like the general coloration of most male ducks, are always conspicuous. It will be further found that the former are definitely *displayed*, the latter usually not. *E.g.*, the display of male ducks is largely a bobbing of the neck ; the general bright body-colour is not made more conspicuous in display. The male duck, furthermore, (i.) takes no share in incubation or rearing the young, (ii.) usually stays near the hen until the young are hatched, (iii.) as soon as he leaves the hen, moults into eclipse (protective) plumage. (iv.) The hen is protectively coloured. (v.) The species is highly palatable and much attacked by Raptores.

Thus there is a good *prima facie* case for applying Dr. Mottram's ideas to cases of bright coloration in the males of palatable species in which the bright colour is not specially associated with display, and especially in forms in which the female alone looks after eggs and young.

It is, however, becoming clear that many side issues of the problem can best be attacked by statistical methods; and this I propose to do as opportunity offers.

POSTSCRIPT 2.—The last number of 'British Birds' (vol. xvi. p. 318) contains an article by Mr. N. Gilroy on the nesting habits of the Black-throated and Red-throated Divers to which reference should be made.

The Black-throated Diver is mentioned as dipping its bill in the water when nervous because scared off its eggs. This extends my observations of the beak-dipping of the Red-throated Diver to another species.

Of courtship, the following remark is made—"The pairs may be observed on the tarns for a considerable time before nesting begins, and one is frequently treated to the extraordinary display which takes place, not only during courtship and pairing, but even when actual breeding has commenced—when both birds propel themselves through the water almost vertically." This, so far as it goes, confirms my observations.

J. S. H.

8th May, 1923.

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- SELOUS. '09. Zoologist (4), xiii. & xiv. (Blackcock.)
- SELOUS. '12 a. Zoologist (4), xvi. p. 81; xvii. p. 210. (Red-throated Diver.)
- SELOUS. '12 b. Zoologist (4), xvi. p. 197. (Origin of Display.)
- SELOUS. '13. Zoologist (4), xvii. (pp. 204, 409). (Swans.)
- SELOUS. '14. Zoologist (4), xviii. p. 73. (Great Northern Diver.)
- SELOUS. '15. Wild Life, vii. (Dabchick.)
- STURTEVANT. '15. Journ. Anim. Behaviour, v. p. 353. (Drosophila.)
- TURNER. '13. Brit. Birds, vii. p. 150. (Red-throated Diver.)
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## EXPLANATION OF THE PLATES.

## PLATE 14.

- Fig. 5. Louisiana Heron (*Hydranassa tricolor*). Twig-bringing ceremony after nest-relief. The relieved bird is presenting a twig to the bird on the nest. Note raising of crest, aigrettes, and neck-feathers, and spreading of wings.
- Fig. 6. Nest-relief ceremony of Little White Egret (*Egretta candidissima*). The bird on the right is about to step off the nest. Note erection of crests and aigrettes, and spreading of wings.

## PLATE 15.

- Fig. 7. Two female Whitethroats (*Sylvia cinerea*) fighting for a male and his territory; the male watching.
- Fig. 8. A pair of Willow-Warblers (*Phylloscopus trochilus*); simultaneous performance of wing-flapping ceremony.



FIG. 5. Louisiana Heron (*Hydromas tricolor*). Twig-bringing ceremony after nest relief. The relieved bird is presenting a twig to the bird on the nest. Note raising of crest, aigrettes, and neck feathers, and spreading of wings. (Photo by J. S. H.)



FIG. 6. Nest-relief ceremony of Little White Egret (*Egretta candidissima*). The bird on the right is about to step off the nest. Note erection of crests and aigrettes, and spreading of wings. (Photo by J. S. H.)





FIG. 7. Two female White-throats (*Sylvia curruca*) fighting for a male and his territory - the male watching.  
Reproduced by permission from E. Howard, 'The British Warblers.'



FIG. 8. A pair of Willow-Warblers (*Phylloscopus trochilus*): simultaneous performance of wing-flapping ceremony.  
Reproduced by permission from E. Howard, 'The British Warblers.'



On Cellularine and other Polyzoa. By Sir SIDNEY F. HARMER, K.B.E.,  
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(PLATES 16 19.)

[Read 1st February, 1923.]

### I. INTRODUCTION.

THE collection of the Polyzoa made by the 'Siboga' in Malay waters is perhaps the most important one which has been obtained in any part of the world since the 'Challenger' Expedition, including as it does representatives of the shallow and deep water Fauna of a district rich in Polyzoa, but at present very imperfectly known. A study of the representatives of this group in the area in question is specially needed, in order to fill a conspicuous gap in our knowledge. The Polyzoa of parts of Australia have perhaps been more fully studied than those of any other part of the world, with the exception of the Atlantic and Arctic areas; particularly those of Victoria and New South Wales, thanks to the labours of Busk, Hincks, MacGillivray, Waters, and others. Those of Japan have been described, to some extent, by Ortmann, and are receiving attention from Yanagi and Okada. Hincks and Miss Robertson have described some of the Polyzoa of the Pacific coast of North America, but those of the Pacific in general have been very imperfectly investigated, although some information on the subject has been given by Westphal. Waters has published two important papers on the Polyzoa of the Red Sea and East Africa, and Savigny's admirable figures of Egyptian species, some of which were obtained in the Red Sea, as well as a recent paper by Marcus on South African species, must be specially noticed. Hincks has described Polyzoa from the Indian Ocean, particularly from the Mergui Archipelago; and Miss Thornely and Miss Robertson have also made contributions to our knowledge of the Polyzoa of this Ocean.

In investigating the Cheilostomata of the Malay Archipelago, I have found it necessary to devote much attention to various questions which do not form a necessary part of the Report which is in preparation. I have been obliged in particular to study various genera, in order to attempt to decide their characters and the names which ought to be assigned to them.

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In dealing with these questions I have had the great advantage of being able to make use of the important type-specimens, particularly those of Busk, in the British Museum. Some of the results thus obtained are given in the present paper, which is intended to be preliminary to my fuller Report. The genera considered are those of the "Cellularine" series, together with others which have to be discussed in connection with these. For the purposes of this general survey I am obliged to give diagnoses of several new genera; but I restrict myself to those which are strictly necessary, believing as I do that the practice of publishing preliminary diagnoses which cannot be fully understood without adequate illustration is one to be avoided as much as possible. I devote special attention to species which have been included in the genus *Menipea*; and I venture to think that the grouping here suggested, in this and other genera, will give greater precision to certain questions of Geographical Distribution. I desire to acknowledge specially the valuable assistance I have received from my colleagues Mr. C. Davies Sherborn and Mr. R. Kirkpatrick. Mr. Sherborn has helped me particularly with regard to the dates of publication of various Memoirs, while his invaluable MS. list, at present in course of publication (*Index Animalium*, 1801-1850) by the Trustees of the British Museum, has been of special assistance in ascertaining that several genera in current use are preoccupied. Mr. Kirkpatrick, who is in charge of the Collection of Polyzoa in the British Museum, has given me much appreciated help in referring to the specimens, and in other ways. Special attention may be directed to Sect. III. (Internal avicularia) and Sect. IV. (Methods of bifurcation).

The present paper is divided into the following Sections:—

- I. Introduction.
- II. Literature and Nomenclature.
- III. Internal avicularia.
- IV. Methods of bifurcation of the colony.
- V. Characters of certain genera and species of *Scrupocellariidæ*.

## II. LITERATURE AND NOMENCLATURE.

This Section includes a list of Memoirs to which shortened references are given throughout the paper; but full references are given, in their proper places, to many other works not included in the list. The Bibliography is followed by an alphabetical list of genera, in which I have endeavoured to establish the respective genotypes, where this has not already been done. In constructing this list I follow the example which has been given by Lang (1917, *Geol. Mag.*, Dec. vi, vol. iv. p. 169). I have also indicated, as far as possible, the names which appear to me synonymous with genera of earlier

introduction. The consideration of a number of genera at the same time has had great advantages, by enabling many cases to be discovered in which the conclusions drawn from the study of one genus by itself are modified by taking others into account. I have found it necessary to propose the following new genera and species in the present Section :—

*Camptoplites*, n. gen.

*Didymozoum*, nom. nov., to replace *Didymia*, pre-occupied.

*Euoplozoum*, n. gen.

*Himantozoum*, n. gen.

*Onchoporella buskii*, nom. nov., for *Onchoporella bombycina*, Busk.

*Stirpariella*, nom. nov., to replace *Stirparia*, pre-occupied.

The following new names are proposed in Sect. V. :—

*Anastigia kirkpatricki* (Levinsen, MSS.), n. sp.

*Menipea rectifera*, n. sp.

*Notoplites*, n. gen., and *N. rostratus*, n. sp.

I accept the main divisions of the Cheilostomata which were suggested by Levinsen (1909, pp. 88–90). The Order is divided into two Sub-Orders : (1) *Anasca*, in which the original frontal membrane persists, wholly or in part, in a membranous condition ; (2) *Ascophora*, in which a compensation-sac is present (cf. Harmer, Q. J. M. S. xlv. p. 263). The *Anasca* are further subdivided into three Divisions : (i.) *Malacostega*, with the frontal membrane for the most part in its primitive, membranous condition ; (ii.) *Coilostega*, with a considerable development of a calcareous layer, the cryptocyst, subjacent to the frontal membrane, and frequently pierced by foramina, the opesiules, traversed by the tendons of the depressor muscles, which are inserted into the frontal membrane ; (iii.) *Pseudostega*, with peculiar, immersed ovicells and certain other characters, consisting mainly of the Family *Cellariidæ*.

The genera included in the following list are mainly the erect branching forms of the *Anasca*. I have included all Levinsen's Families of recent *Malacostega*, with the exception of the *Membraniporidæ* and *Cribrilinidæ* ; the erect, branching genera of the *Coilostega*, but not the encrusting forms nor those with an *Escharine* habit ; and the genera of recent *Pseudostega*. The Cellularine assemblage, with which I am principally concerned, consists of the branching, erect genera of the *Malacostega*. The branching *Ascophorous* genera, such as the *Catenicellidæ*, provided with a compensation-sac, are not included in my list, with one or two exceptions, in the case of names which have some bearing on the nomenclature of other genera under consideration.

## A. LITERATURE.

*Abbreviations:—*

A. M. N. H.—Annals and Magazine of Natural History.

A. S. N.—Annales des Sciences Naturelles (Zoologie).

J. L. S.—Journal of the Linnean Society (Zoology).

P. F. T. C.—See under D'Orbigny.

Q. J. M. S.—Quarterly Journal of Microscopical Science.

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## B. NOMENCLATURE.

- Acamarchis*, Lamouroux, 1816, p. 132.—Genosyntypes, *A. neritina* (L.) and *A. dentata*, Lamx., n. sp. Genolectotype, *Acamarchis neritina* (*Sertularia neritina*, L., 1758, p. 815), a selection which may be considered to have been made by Schweigger, 1819, Tab. 8; 1820, p. 429; with erroneous citation as *neretina*. It may be noted that D'Orbigny (1852, P. F. T. C. p. 323) gives 1812 as the date of introduction of *Acamarchis*; but his synonymy on the following page shows that he referred to Lamouroux, 1816. I regard *Acamarchis* as a synonym of *Bugula*, Oken, 1815, in accordance with the practice of most modern authorities.
- Aetea*, Lamouroux, 1812, p. 184.—Genotype (the only species), *Aetea anguina* (*Sertularia anguina*, L., 1758, p. 816).
- Asteopsis*, Boeck, 1862, Forh. Vid.-Selsk. Christiania, Aar 1861, p. 49 (also given as *Aetiopsis*).—Genotype (the only species), *Asteopsis elongata*, Boeck, n. sp., which is regarded by Smitt, 1868, p. 280, as a synonym of *Aetea truncata*, Landsborough. Synonym of *Aetea*, Lamouroux, 1812.
- Aetiopsis*.—See *Asteopsis*.

- Alysidium*, Busk, 1852<sup>2</sup>, p. 13.—Genosyntypes, *A. parasiticum*, Busk, n. sp., and *Eucratea lafontii*, Audouin, 1826, p. 242; 1828, p. 74. Genoelectotype, *Alysidium parasiticum*, see Norman, 1909, J. L. S. xxx. p. 295.
- Amastigia*, Busk, 1852<sup>2</sup>, p. 40.—Genotype (the only species), *Amastigia nuda*, Busk, n. sp.
- Anderssonia*, Kluge, 1914, p. 617.—Genotype (the only species), *Anderssonia antarctica*, Kluge, n. sp. Synonym of *Amastigia*, Busk, 1852; but pre-occupied by *Andersonia*, Boulenger (Pisces), 1900, A. M. N. H. (7) vi. p. 528, and by *Anderssonia*, Strebel (Mollusca), 1908, Wiss. Ergebn. Schwed. Südpolar-Exp. vi. 1, p. 12.
- Anguinaria*, Lamarck, 1816, p. 142.—Genotype (the only species definitely mentioned), *Anguinaria spatulata*, Lamk., nom. nov. Lamarck gives *Sertularia anguina*, L. (1758, p. 816) as a synonym, from which it appears that the introduction of a new trivial name was unnecessary. Hincks (1880, p. 2) states that *Anguinaria* was mentioned, but not defined, by Lamarck in 1812; but on consulting this work (Extr. Cours Zool. Mus. Paris, p. 24) it is found that Lamarck did no more than mention the generic name in the French form "Anguinaire." Synonym of *Aetea*, Lamx., 1812.
- Angularia*, Busk, 1881, Q. J. M. S. xxi. p. 14.—Mentioned as an abyssal genus with a web-like expansion at the angle of most of the bifurcations. No species is indicated, and the genus does not seem to have been referred to by Busk in any later work.
- Avicella*, Van Beneden, 1848, Bull. Acad. roy. Belg. xv. 1, p. 74.—Genosyntypes, 5 species, all referable to *Bugula*, Oken, 1815. As this is the case, there seems to be no object in selecting a genotype, which it would be difficult to do in view of uncertainty as to the identification of some of the species described.
- Avicularia* (Thompson, MSS.), Gray, 1848, pp. 105, 146.—Genotype (the only species), *Avicularia flabellata* (Thompson, MSS.), Gray, n. sp. Synonym of *Bugula*, Oken, 1815; but pre-occupied by *Avicularia*, Lamarck (Arachnida), 1818, An. s. Vert. v. p. 107.
- Bactridium*, Reuss, 1848, Naturwiss. Abhandl. (Haidinger), ii. p. 55.—Genosyntypes, *B. hagenowi*, Reuss, n. sp., and 3 other fossil species. Genoelectotype, selected by D'Orbigny, 1852, P. F. T. C. p. 363, and A. S. N. (3) xvii. p. 289, *Bactridium hagenowi*. This species does not seem to belong to the Cellularine assemblage, but the other three species described by Reuss were regarded by D'Orbigny as species of *Canda*.
- Beania*, Johnston, 1840, A. M. N. H. v. p. 272.—Genotype (the only species), *Beania mirabilis*, Johnst., n. sp. See also Johnston, 1847, p. 371.
- Bicellaria*, de Blainville, 1830, p. 423; see also 1834, p. 459.—Genosyntypes, 7 species, including "*B. ciliata*, Ellis" (*Sertularia ciliata*, L., 1758, p. 815). In his revision of genera, Gray (1848, p. 112) includes *B. ciliata* by itself in *Bicellaria*; and, although he gives no diagnosis, by placing *Sertularia ciliata*, L., at the head of his synonymy, he may fairly be considered to have indicated

*Bicellaria ciliata* as the genotype. Pre-occupied by *Bicellaria*, Macquart (Diptera), 1823, Rec. Trav. Soc. Amat. Sci. Lille, Années 1819-1822, p. 155, and replaced by *Bicellariella*, Lev., 1909 (*q. v.*). See also *Bugula*.

*Bicellariella*, Levinsen, 1909, p. 431.—Proposed to replace *Bicellaria*, de Blainville, 1830, pre-occupied (see *Bicellaria*), with genotype *Bicellariella ciliata* (see p. 110).

*Bicellarina*, Levinsen, 1909, p. 99.—Genotype (the only species), *Bicellarina alderi* (*Bicellaria alderi*, Busk, 1860, Q. J. M. S. viii. p. 213).

*Bifrons*, MacGillivray, 1860, Trans. Phil. Inst. Vict. iv. p. 163.—Proposed to replace *Dimetopia*, Busk, 1852, at Dr. Mueller's suggestion, on the ground that *Dimetopia* is used in Botany (Umbelliferae). The alteration is not required by the accepted rules.

*Brettia*, Dyster, 1858, Q. J. M. S. vi. p. 260.—Genotype (the only species), *Brettia pellucida*, Dyst., n. sp.

*Bugula*, Oken, 1815, p. 89.—Genosyntypes, *Cellularia neritina*, *Cell. ciliata*, and *Bugula avicularia* (authorities not cited). Linnæus (1758, p. 809) founded *Sertularia avicularia* primarily on the biserial species figured by Ellis (1755, pl. 20. fig. A), and to this species the Linnean name is now restricted; but he also included the pluriserial species of the same author (*t. cit.* pl. 38. fig. 7), though wrongly citing the Plate as 28. Gray (1848) made *S. avicularia* (*s. str.*) the genotype of a new genus, *Bugulina* (p. 114), while (p. 106) he described the pluriserial species of Ellis, whose Plate is wrongly cited as 58, as *Avicularia flabellata* (Thompson, MSS.), *A. flabellata* being the genotype. He appears to have overlooked the fact that Oken described *C. avicularia* as having its zoecia in 3 or 5 series, as he includes Oken's species in his synonyms of *Bugulina avicularia*, whereas it should properly have come under *Avicularia flabellata*. *B. neritina*, *B. avicularia*, and *B. flabellata* are congeneric, whatever the generic name adopted for them.

In 1819 Schweigger made *Sertularia neritina*, L., the genotype of *Acamarchis* (*q. v.*), to which *S. avicularia*, L., and *Avicularia flabellata* (Thompson, MSS.), Gray, might also be considered to belong. This would necessitate regarding *S. ciliata*, L., as the genotype of *Bugula*, a course which would introduce the greatest confusion into nomenclature. I regard this as an instance in which it is essential to disregard the strict application of the Rules of Nomenclature and to accept Hincks' selection (1880, p. 75) of *Bugula neritina* as the genotype of Oken's genus. As this species is also the genotype of *Acamarchis*, it becomes necessary to choose between the two genera. I give the preference to *Bugula*, partly because it antedates *Acamarchis* by a year, and partly because it has been universally accepted. As a further motive, it may be pointed out that *A. neritina*, in its typical form, is devoid of avicularia, and that certain writers have accepted *Acamarchis* as a genus differing from *Bugula* by the absence of these organs. See also *Bicellaria*.

*Bugularia*, Levinsen, 1909, pp. 99, 108.—Genotype (the only species), *Bugularia dissimilis* (*Carbacea dissimilis*, Busk, 1852<sup>1</sup>, p. 51).

- Bugulella*, Verrill, 1879, Amer. J. Sci. Arts, (3) xvii. p. 472.—Genotype (the only species), *Bugulella fragilis*, Verr., n. sp., described as allied to *Bicellaria* and perhaps to *Brettia*.
- Bugulina*, Gray, 1848, p. 114.—Genotype (the only species), *Bugulina avicularia* (*Sertularia avicularia*, L., s. str.). The form indicated by Gray is the biserial species of Ellis (1755, p. 36, pl. 20. figs. *a*, *A*), to which the trivial name of Linnæus is now restricted. See *Bugula*, of which this genus is a synonym.
- Bugulopsis*, Verrill, 1880, Proc. U.S. Nat. Mus. ii. (1879), p. 190.—Genotype, selected by the author, *Bugulopsis peachii* (*Cellularia peachii*, Busk, 1851, A. M. N. H. (2) vii. p. 82). Synonym of *Tricellaria*, Fleming, 1828.
- Caberea*, Lamouroux, 1816, p. 128.—Genosyntypes, *C. pinnata* and *C. dichotoma*, Lamx., n. spp., both from "Australasie." Genoelectotype, *C. dichotoma*, see Schweigger, 1819, Tab. 9; 1820, p. 430; and Gray, 1848, p. 147.
- Caberiella*, Levinsen, 1909, pp. 134, 135.—Genotype (the only species), *Caberiella benemunita* (*Menipea benemunita*, Busk, 1884, p. 19). Synonym of *Anastigia*, Busk, 1852.
- Caberoïdes*, Canu, 1908, Ann. Paléont. iii. p. 87 (83, sep.).—Genotype, selected by the author, *Caberoïdes canaliculata*, Canu, n. sp. The genus is described as resembling *Caberea* and also members of the Lepralioid series (Hippoporinæ).
- Camptoplites*\*, n. gen.—Genotype, *Camptoplites bicornis* (*Bugula bicornis*, Busk, 1884, p. 40). I propose this genus for Sect.  $\beta$  of *Bugula* as given in Busk's 'Challenger' Report, 1884, p. 37, with the following diagnosis:—
- Zoarium stalked, the stalk prolonged basally into an attaching tuft of rootlets. Zoœcia biserial or pluriserial, narrow proximally, the opesia occupying most of the expanded distal portion. Proximal ends of the zoœcia not forked. Avicularia borne on long, flexible stalks, which usually exceed the head of the avicularium in length. Operculum distinguishable, ovicells well developed.
- The peculiarities of the avicularium and the absence of a forked proximal end in the zoœcia seem to justify generic separation for this assemblage of forms, which are characteristic of abyssal depths and of the Antarctic area. In addition to the type-species and *B. reticulata*, described by Busk in his original account, the following species are referable to *Camptoplites*:—*Bugula tricornis*, Waters, 1904, "Belgica" Bryozoa, p. 23; and the following species described by Kluge (1914):—*Bugula bicornis*, vars. (pp. 619–624), *B. areolata* (p. 627), *Bugula* sp., var. *variospinosa*, nov. (p. 628), *B. multi-spinosa* (p. 628), *B. retiformis* (p. 629), *B. levaldi* (p. 630), *B. gigantea* (p. 630), *B. angusta* (p. 631), *B. abyssicola* (p. 632), and *B. lata* (p. 634), Kl., n. spp.
- Canda*, Lamouroux, 1816, p. 131.—Genotype (the only species), *Canda arachnoides*, Lamx., n. sp.

\* *καμπτός*, flexible; *δολίχης*, an armed man; in allusion to the long, flexible stalk of the avicularium. The genus is masculine.

*Carbacea*, Gray, 1848, pp. 105, 146.—The only species is *Carbacea papyracea*, but the synonymy includes the following species:—(1) *Eschara papyrea*, Pallas (1766, p. 56), from the Mediterranean, still known by Pallas' trivial name; (2) *Flustra carbacea*, Ellis and Solander (1786, p. 14), from Aberdeen and Edinburgh. By the rule of absolute tautonymy the genotype is *F. carbacea*, and this conclusion is confirmed by Gray's mention of specimens from Northumberland and Scarborough examined by him in the British Museum Collection. The genotype has been renamed *C. solanderi* by Norman (1903, A. M. N. H. (7) xi. p. 582), but there appears to be no valid reason for rejecting its original name, which should accordingly stand as *Carbacea carbacea* (Ell. and Sol.).

*Caulibugula*, Verrill, 1900, Trans. Conn. Acad. x. p. 593.—Genotype, selected by the author, *Caulibugula armata*, Verr., n. sp. Apparently a synonym of *Stirpariella* (q. v.).

*Cellaria*, Ellis and Solander, 1786, p. 18.—Genosyntypes, 18 species, referable to about 13 modern genera. Thirteen of these species are identical with species included by Pallas in *Cellularia* (q. v.), as is shown by the identical citations, by both authors, of the work of Ellis (1755). It has generally been assumed that *Cellaria* was a gratuitous alteration of *Cellularia*; but Ellis and Solander do not refer to Pallas, and it seems possible that their arrangement was an entirely independent one, based on the works of Ellis and Linnaeus.

In 1801 Lamarek (Syst. An. s. Vert. p. 382) defined *Cellaria* nearly in its modern sense, including two species only:—(1) *C. salicornia*, with synonyms *C. farciminoïdes*, Ell. and Sol. and *Tubularia fistulosa*, L.; (2) *C. cirrata*, Ell. and Sol., which later became the genotype of *Menipea* (q. v.). He placed *C. salicornia* alone in the first Section of the genus, distinguished by having "Articulations couvertes de cellules dans tous les sens." Under *Cellaria* Lamouroux (1816, p. 125) moreover writes: "J'ai conservé le nom de Cellaire au groupe dont les Polypiers avoient pour type le *Cellaria Salicornia*."

I think this is a case in which the strict Law of Priority should be set on one side, in view of the undoubted inconvenience of reverting to the earlier name. Norman (1903, A. M. N. H. (7) xi. p. 577) suggested a return to *Cellularia*, pointing out that *Cellaria* is to be regarded as an absolute synonym of that genus. But, on the other hand, *Cellaria* had already acquired a definite signification, which it has since retained; and this cannot be said of *Cellularia*, which has been used in the most various senses, and should, in my opinion, be discarded. In this respect I am in agreement with the conclusions of D'Orbigny (1851, P. F. T. C. p. 27), Smitt (1868, p. 383), Hincks (1880, p. 104), Waters (1897, J. L. S. xxvi. p. 3), and others. The genotype is *Eschara fistulosa*, L., of which *C. farciminoïdes*, included in Ellis and Solander's original account, as well as *Cellularia salicornia* (pars), Pallas, selected by Lamouroux (1816) as the genotype, are synonyms.

The identification of the species to which the Linnean name *fistulosa* properly belongs requires further consideration, and the conclusion at which I have arrived is not the one ordinarily accepted. *Eschara fistulosa* was



introduced by Linnæus (1758, p. 804) in his 10th Edition, with references to Ellis (1755, p. 46, no. 1, pl. 23. fig. A), followed by citations of Bauhin, Ray, Plukenet, and Barrelierus. In his 12th Edition (1767, p. 1302) Linnæus describes the same species as *Tubularia fistulosa*, with one or two additional citations. Pallas (1766, p. 61), in introducing *Cellularia salicornia*, gives all the citations of Linnæus (1758), with others, but he includes two species under one name. Ellis and Solander (1786, p. 26) describe *Cellaria farciminoïdes*, with citations of Ellis (p. 46, pl. 23) and of *Tubularia fistulosa*, L., 1767. It is quite clear that the three trivial names, of Linnæus, Pallas (in part), and Solander, respectively, refer to one and the same species.

The examination of the original works cited by Linnæus in 1755 shows, however, that his synonymy is open to a good deal of criticism. The figures of Ellis refer unquestionably to a species of *Cellaria* as here understood. Bauhin and Cherler (1651, Hist. Plant. iii. p. 811) describe two forms, a coarser species, from the Adriatic, and a more slender "varietas," of which the locality is not given. The coarser species, to which Linnæus expressly limits his reference ("Corallina fistulosa fragilis crassior"), shows projections on the internodes which suggest the produced peristomes of *Tubucellaria*, to which genus I have little doubt that it belonged. The slenderer species was probably a *Cellaria*. Ray (1686, Hist. Plant. i. p. 65) quotes Bauhin and Cherler *verbatim*, without giving additional information. Plukenet (1696, Almagestum Botanicum, p. 118, pl. 26. fig. 2) also cites Bauhin and Cherler. His figure might refer to a *Cellaria*, but his collection is in the Sloane Herbarium at the British Museum (Natural History), and his specimen, preserved in Vol. 95, Fol. 194 of that Collection, is a Coralline Alga. Barrelierus (1714, Plantæ per Galliam, Hispaniam et Italiam observatæ, p. 121) quotes Bauhin and Cherler and Ray. He describes and figures a coarser and a slenderer form, but the coarser species may be an Alga, although the other is probably a *Cellaria*. In view of these discrepancies and uncertainties it is necessary to regard the citation of Ellis, the first on the list, as the one to which Linnæus' name really refers; and this conclusion is confirmed by the fact that he consistently made use of Ellis' admirable figures in describing branching Polyzoa, many of his species being introduced with a citation of Ellis and of no other author.

Ellis explicitly states that there are two species of his "Bugle Coralline," and he is equally definite in explaining that his figures *a*, *A*, *B*, and *C* belong to the "larger Bugle Coralline." *D*, the remaining figure on his Pl. 23, appears to belong to the same species, though this is not stated quite so definitely. The mere question of size indicates that Ellis' figured species is the one usually described as *Cellaria sinuosa*, and that Ellis' smaller species is the *C. fistulosa* of Hincks and of other modern authors.

*C. sinuosa* was introduced, as *Farcimia sinuosa*, by Hassall (1840, A.M.N.H. vi. p. 172, pl. 6. figs. 1, 2), who expressly states that it is larger than what he calls *F. salicornia* (Ellis' smaller species), and that it is distinguished by having its apertures in the upper third of the cell. This character is clearly

shown by Ellis in his figs. B and D. Hassall later (1843, A. M. N. H. xi. p. 112) altered the name of his species to *F. spathulosa*.

In regarding *Cellularia fistulosa* as the genotype of the genus I am obliged to accept the following synonymy:—

1. *CELLARIA FISTULOSA* (L.).

Larger Bugle Coralline, Ellis, 1755, p. 46, pl. 23. figs. *a*, A-D.

*Eschara fistulosa*, L. 1758, p. 804.

*Cellularia salicornia* (*pars*), Pallas, 1766, p. 61.

*Tubularia fistulosa*, L. 1767, p. 1302.

*Cellularia farciminioides*, Ellis and Solander, 1786, p. 26.

*Tubularia salicornis* (*fistulosa*) (*Cellaria salicornea*, Pall.), Esper, between 1805 and 1810, Pflanzenth. iii. p. 103, *Tubularia*, pl. 2. figs. 1-4 (figures poor, but Ellis cited in synonymy).

*Salicornaria dichotoma*, Schweigger, 1819, Tab. 8: 1820, p. 428.

*Farcimia sinuosa*, Hassall, 1840, A. M. N. H. vi. p. 172, pl. 6. figs. 1, 2.

*Farcimia spathulosa*, Hassall, 1843, A. M. N. H. xi. p. 112.

*Cellaria sinuosa*, Hincks, 1880, p. 109.

(nec *Cellaria fistulosa*, Hincks, 1880, p. 106; and of other authors.)

2. *CELLARIA SALICORNIA* (Pallas).

*Cellularia salicornia* (*pars*), Pallas, 1766, p. 61.

? *Cellaria salicornioides*, Lamouroux, 1816, p. 127.

*Salicornaria farciminioides*, Johnston, 1847, p. 355.

*Cellaria fistulosa*, Hincks, 1880, p. 106; *et auctt.*

Pallas divided *C. salicornia* into two Sections:—(α) the larger Bugle Coralline, as shown by his citation of Ellis, Pl. xxiii.; (β) a more slender form, characterized in his synonymy as “subtilior” and “tenuior,” in contrast with “crassior” of his first Section. He gives *Eschara fistulosa*, L., as a synonym of β, but this was not admissible, in view of Linnaeus’ citations of Ellis’ figure of the larger Bugle Coralline and of the “*Corallina fistulosa fragilis crassior*” of Bauhin and Cherler, emphasizing the fact that he had the coarser form in mind. This conclusion is not modified by reference to Linnaeus’ “*Fauna Svecica*,” 1761, no. 2232, which Pallas wrongly cites as 2234. Pallas includes Ellis “*Angl. Bugle Coralline*” at the end of his Sect. β, and this may be taken as the determining factor. As his trivial name is not applicable to the larger Bugle Coralline, it may be used for the smaller form. The adoption of *C. salicornioides* for this species would be open to some uncertainty, as though Lamouroux also had a slender species in view, the locality, presumably of specimens in his own collection, is given as Mediterranean. This suggests the possibility that his specimen, if it exists, may prove to belong to *C. (Nellia) johnsoni*, Busk (1858, Q. J. M. S. vi. p. 125), the typical locality of which is Madeira, and not to *C. fistulosa*, auctt.

*Cellarina*, Van Beneden, 1848, Bull. Acad. Roy. Belg. xv. 1, p. 70.—Genosyntypes, *C. gracilis* and *C. scabra*, Van Ben., n. spp., and *Crisia delilii*, Audouin, 1826, p. 242. Norman (1903, A. M. N. H. (7) xi. p. 579), who had examined a fragment of Van Beneden’s type-specimen of the first species, described it as

*Menipea gracilis*, but admitted its identity with *Cellularia ternata*, forma *gracilis*, Smitt (1868, p. 283). Whether *C. gracilis* is to be regarded as a species or as a variety, it clearly belongs to *Tricellularia*, Fleming, 1828; while the other two species are referable to *Scrupocellularia*, Van Beneden, 1845.

*Cellarina*, D'Orbigny, 1851, P. F. T. C. p. 181; see also 1852, A. S. N. (3) xvi. p. 336.—Genosyntypes, two fossil species. Pre-occupied by *Cellarina*, Van Beneden, 1848.

*Cellularia*, Pallas, 1766, p. 58.—Genosyntypes, 18 species, referable to about 12 genera. The name has been used by many modern authorities, but in the most various senses, and it has been impossible at present to come to any agreement as to the use which should be made of it. The selection of *C. scruposa* as the genotype, by Verrill (1880, Proc. U.S. Nat. Mus. ii. (1879) p. 190) is invalidated by the fact that this species was already the genotype of *Scrupocellularia*, Van Beneden, 1845. I consider it desirable to suppress *Cellularia* in favour of *Cellariu* (q. v.).

*Cercaripora*, Fischer, 1866, C. R. Acad. Sci. Paris, lxii. p. 987; Nouv. Arch. Mus. Hist. Nat. ii. p. 312.—Genosyntypes, *Anguinaria truncata*, Landsborough, 1852, Hist. Brit. Zooph. p. 288; *Aetea ligulata*, Busk<sup>2</sup>, p. 31; and *Aetea argillacea*, Smitt, 1866, Öfv. K. Vet.-Akad. Förh. xxii. (1865) p. 29. The genus was placed in a different Family from that containing *Aetea*, which Fischer restricted to *Sertularia anguina*, L. (1758, p. 816); but later authors have regarded it as a synonym of *Aetea*, of which this species is the genotype.

*Chaperia*, Jullien, 1881, Bull. Soc. Zool. France, vi. pp. 163, 164.—Although the author mentions *Membranipora* (*Steganoporella*) *maynilabris*, Busk (1854, Brit. Mus. Cat. ii. p. 62), as belonging to *Chaperia*, the genotype selected by him on p. 164 is *Chaperia australis*, nom. nov., to replace *M. spinosa*, Q. and G., as quoted by Busk (1879, Phil. Trans. vol. 168, p. 195), in describing specimens from Kerguelen. Jullien gives a description of *C. australis*, from specimens obtained at the Cape of Good Hope. But Busk's citation was a mistake, the species described by Quoy and Gaimard (1824, Zool. Voy. Uranie et Physicienne, p. 605) from the Falkland Is. having been named by them *Flustre épineuse*, *Flustra acanthina*; see Waters, 1898, J. L. S. xxvi. p. 673; see also Marcus, 1922, Göteborgs K. Vet.- och Vitt.-Samh. Handl. (4) xxv. p. 6. Jullien's name *australis* was proposed on the ground that *spinosa* was pre-occupied; but if *C. australis* is synonymous with Quoy and Gaimard's species, the name of the genotype should be *Chaperia acanthina* (Q. and G.).

*Chartella*, Gray, 1848, pp. 104, 145.—Genotype (the only species), *Chartella papyracea* (*Flustra papyracea*, Ellis and Solander, 1786, p. 13).

*Chaunosia*, Busk, 1867, Q. J. M. S. (n. s.) vii. p. 241.—Genotype (the only species), *Chaunosia hirtissima*, Busk, n. sp. Although Busk expressly marks his species as "n. sp.," he adds that it is not unlikely to be identical with *Diachoris hirtissima*, Heller (1867, Verh. Zool.-Bot. Ges. Wien, xvii. Abhandl. p. 94). Synonym of *Beania*, Johnston, 1840.

*Chlidonia*, Lamouroux, 1824, p. 192.—Lamouroux states that Savigny's species (see below) appears to be the *Vorticella polyppina* "des auteurs," and the author he had specially in mind may well have been Esper, who uses this name in Th. ii. of the Forsetz. d. Pflanzenth., *Vorticella*, Pl. 1. figs. 1, 2. The text of this part of the "Fortsetzungen" ends with p. 48, and it contains no description of the plate in question. It was published in two Lieferungen, 9 and 10, in 1798 and 1806, respectively. The plate presumably appeared between 1798 and 1810, the date of Esper's death.

The name "*Chlidonias*" was used by Savigny (Description de l'Égypte), at the foot of his Pl. 13, in which figs. 3<sup>1</sup>-3<sup>5</sup> give admirable representations of what is almost certainly the same species as *Vorticella polyppina*, Esp. Audouin, in his "Explications" (1826, p. 243) of Savigny's plates, did not, however, accept Savigny's name, as he describes the species figured as *Eucratea cordieri*. Lamarck (1816, p. 140) introduced a new name, *Cellaria vesiculosa*, with *Vorticella polyppina*, Esp. as a synonym, but with a query; and Hammer (1829, in Esper, Pflanzenth. iii. Lief. 16, p. 255) uses *Eucratea vesiculosa* in describing Esper's plate. Lamarck's trivial name antedates Audouin's, but Bertoloni (1810, Rar. Ital. Plant., Decas Tertia, p. 112; see also 1819, Amoen. Ital. p. 273) had previously described the same species as *Cellaria pyriformis*, in both papers giving a recognizable description of *Chlidonia*, based on actual specimens. His 1810 synonymy refers to *Vorticella polyppina*, L. (1767, p. 1317), an Infusorian. In 1819 he cited Esper's figures, thereby making his descriptions more intelligible; while by rejecting his earlier synonymy he furnished a justification for the introduction, otherwise invalid, of a new trivial name in 1810.

The genotype thus appears to be *Chlidonia pyriformis* (Bert.), of which the other names indicated above are synonyms. *Chlidonia*, Lamx., 1824, antedates both *Chlidonia*, Hübner, 1825-1826\* (Verz. bekannt. Schmetterl. p. 393) and *Chlidonia*, Herrich-Schäffer, 1838 (in Panzer, Deutschl. Insecten, Heft 157), two genera of Insects. *Chlidonias* was introduced by Rafinesque, 1822 (Kentucky Gazette, xxxvi. (8) p. 3), and this name is regarded as valid by Ornithologists. There seems to be no inconvenience in retaining *Chlidonia* for Polyzoa, in spite of its close resemblance to the name of a genus of Birds.

*Cinetoskian*, von Martens, 1879, Zool. Rec. for 1877, xiv. Molluscoida, p. 94.—An emendation proposed by von Martens, in recording the introduction of *Kinetoskias* (q. v.). Although the name might have been thus spelt it is undesirable to alter the accepted original form.

*Columnaria*, Levinson, 1909, p. 116.—Introduced for *Columnaria borealis*, n. sp., and all the species of *Farciminaria* described by Busk (1884, pp. 48-51), except *F. atlantica*. No genotype was selected, but this is of small importance, since the name is pre-occupied, in Authozoa, by *Columnaria*, Goldfuss, 1826, Petr. German. i. pt. 1, p. 72 (for date of publication see Woodward, vol. ii. p. 692). I prefer not to suggest a new name without making a study of the species involved.

\* For the date of publication see Proc. iv. Int. Congr. Zool. (Cambridge, 1898), 1899, p. 299.

- Cornucopina*, Levinsen, 1909, pp. 98, 109.—Levinson states that this genus includes most of the species of *Bicellaria*, auctt., but the only species he definitely refers to it (pp. 110, 372) are *Bicellaria grandis*, Busk (1852<sup>1</sup>, p. 374; 1852<sup>2</sup>, p. 42) and *B. infundibulata*, Busk (1884, p. 33). Of these the latter is exceptional in certain characters, and I think it more convenient to select *Cornucopina grandis* as the genotype.
- Corynoporella*, Hincks, 1888, A. M. N. H. (6) i. p. 215.—Genotype (the only species), *Corynoporella tenuis*, Hincks, n. sp., described as allied to *Bugula*.
- Cothurnicella*, Wyville Thomson, 1858, Nat. Hist. Rev. v., Proc. of Societies, p. 141.—Genotype (the only species), *Cothurnicella dardala*, Wyv. Thoms., n. sp., a synonym of *Cellaria pyriformis*, Bert., the genotype of *Ohlidonia*, Lamx., 1824.
- Craspedozoum*, MacGillivray, 1886, Trans. Proc. R. Soc. Vict. xxii. p. 131.—Genosyntypes, *Membranipora roborata*, Hincks (1881, A. M. N. H. (5) viii. p. 128); *C. ligulatum*, *C. spicatum*, MacG., n. spp., and *Flustra membraniporides*, Busk (1884, p. 54). As I regard this genus as a synonym of *Menipea*, Lamx., 1812, it seems unnecessary to select a genotype.
- Crepis*, Jullien, 1882, Bull. Soc. Zool. France, vii. p. 522.—Genotype (the only species), *Crepis longipes*, Jull., n. sp.
- Crisia*, Lamouroux, 1812, p. 183.—Genosyntypes, *Sertularia eburnea*, L. (1758, p. 810), a Cyclostome, and 5 species of Cheilostomes, including *Sertularia ciliata*, L. (1758, p. 815). Under *Eucratea* I suggest ignoring Schweigger's selection of *C. ciliata* as the genotype. If this proposal is accepted, it will be possible to consider that Fleming (1828, p. 540) selected *Crisia eburnea* as the genotype, by including it, with another species not appearing in Lamouroux's original account, in *Crisia* with an amended diagnosis.
- Crisularia*, Gray, 1848, pp. 111, 147.—Genotype (the only species), *Crisularia fastigiata* (*Sertularia fastigiata*, L. 1758; p. 815 = *Cellularia plumosa*, Pullus, 1766, p. 66). Synonym of *Bugula*, Oken, 1815.
- Dendrobeania*, Levinsen, 1909, pp. 99, 113.—Genotype (the only species), *Dendrobeania murrayana* (*Flustra murrayana* (Bean, MSS.), Johnston, 1847, p. 347. Synonym of *Bugula*, Oken, 1815.
- Diachoris*, Busk, 1852<sup>1</sup>, p. 381.—Genotype (the only species), *Diachoris crotali*, Busk, n. sp. See also Busk, 1852<sup>2</sup>, p. 54. Synonym of *Beania*, Johnston, 1840.
- Diachoseris*, Ortmann, 1889, Arch. f. Naturg. lvi. i. p. 25.—The name appears to be a misquotation of *Diachoris*, Busk, 1852. The following species are included:—*Diachoris magellanica*, Busk (1852<sup>2</sup>, p. 54), *Diachoseris discodermis*, and *D. hexaceras*, Ortm., n. spp. Synonym of *Beania*, Johnston, 1840.
- Didymia*, Busk, 1852<sup>1</sup>, p. 383.—Genotype (the only species), *Didymia simplex*, Bk., n. sp. See also Busk, 1852<sup>2</sup>, p. 35. The genus being pre-occupied, in Hymenoptera, by *Didymia*, Le Peletier and Serville, 1825, Encycl. Méthod. x. (Entomologie), p. 574, I propose to replace it by *Didymozoum*, nom. nov., with the genotype *Didymozoum simplex* (Busk).

*Didymozoum*, nom. nov.—See *Didymia*.

*Dinetopia*, Busk, 1852<sup>1</sup>, p. 384.—Genosyntypes, *D. spicata* and *D. cornuta*, Busk, n. spp. See also Busk, 1852<sup>2</sup>, p. 35. In 1909 Prof. A. Billard submitted to me a specimen of *Dynamena barbata*, Lamx. (1816, p. 178), from Lamouroux' type-collection at Caen; and I convinced myself that *D. spicata*, Busk, was a synonym of this species (see Billard, C.R. Acad. Sci. Paris, 1909, cxlviii. p. 1064). In the apparent absence of an earlier selection I propose *Dinetopia cornuta* as the genotype. It appears to me preferable to select a species of which good figures were published by Busk, rather than to choose *D. barbata*, the identification of which with *D. spicata* rests merely on my own authority.

*Dimorphozoum*, Løvinsen, 1909, pp. 96, 107.—Genotype (the only species), *Dimorphozoum nobile* (*Flustra nobilis*, Hincks, 1891, A.M.N.H. (6) vii. p. 288).

*Diplodidymia*, Reuss, 1869, Sitzb. Akad. Wiss. math.-nat. Cl. lix. i. Abth. p. 468.—Genotype (the only species), *Diplodidymia complicata*, Reuss, n. sp. Synonym of *Poricellaria*, D'Orbigny, 1852.

*Dittosaria*, Busk, 1866, Geol. Mag. iii. p. 301.—Genotype (the only species), *Dittosaria wetherellii*, Busk, n. sp., a fossil, from the London Clay, perhaps allied to *Sertularia loricata*, L., the genotype of *Eucratea* (q. v.).

*Emma*, Gray, 1843, p. 293.—Genotype (the only species), *Emma crystallina*, Gray, n. sp. Gray gave no generic diagnosis, but this was done by Busk, 1852<sup>1</sup>. p. 372, and 1852<sup>2</sup>, p. 27.

*Epistomia*, Fleming, 1828, p. 541.—Genotype, selected by the author, *Epistomia bursaria* (*Sertularia bursaria*, L., 1758, p. 814). See Gregory, 1893, Trans. Zool. Soc. xiii. p. 227. See also *Notamia*.

*Erina*, Canu, 1908, Ann. Mus. Nac. Buenos Aires (3) x. p. 273.—Genotype, selected by the author, *Erina patagonica*, Canu, n. sp., placed in Meliceritidæ. Pre-occupied by *Erina*, Swainson, 1833, Zool. Illustr. (2) iii. pl. 134 (Lepidoptera).

*Eucratea*, Lamouroux, 1812, p. 183.—Genosyntypes, *Cellaria cornuta* (*Sertularia cornuta*, L., 1758, p. 810) and *C. loricata* (*Sertularia loricata*, L., 1758, p. 815). In the same Memoir Lamouroux introduced the genus *Crisia* (q. v.). Each of these genera included one species, *S. cornuta* and *S. eburnea* respectively, belonging to *Crisia* as universally understood at the present time. It is unfortunate that Schweigger (1819, Tab. 8; 1820, p. 429) indicated *S. cornuta* as the genotype of *Eucratea*, and *S. ciliata* as the genotype of *Crisia*; both of Lamouroux' genera being regarded by him as subgenera of *Cellularia*. By adopting these selections *Bicellaria*, auctt., would become a synonym of *Crisia*, and *Crisia*, auctt., of *Eucratea*. These alterations would be so inconvenient and confusing that I feel justified in suggesting that Schweigger's selections should be ignored. If *Crisia* is to be maintained, its genotype must be *Crisia eburnea* (Linn.), and *S. cornuta* will fall within the same genus; *Eucratea loricata* (Linn.) thus remaining as the genotype of *Eucratea*. *S. chelata*, L. (1758, p. 816), which has usually been regarded as the genotype of *Eucratea*, has no claim to this position, as it was not included in *Eucratea* by Lamouroux until 1816 (p. 149).

*Eucrateria*, Fleming, 1828, p. 541.—Used by mistake for *Eucratea* (q. v.).

*Euoplozoum*\*, n. gen.—Genotype, *Euoplozoum cirratum* (*Cellularia cirrata*, Busk, 1884, p. 17).

Zoarium erect, attached by a basal tuft of rootlets. Branches biserial, the zoecia large and obliquely alternating, all facing in the same direction, their proximal portions narrow, their distal portions expanded, the frontal membrane occupying the entire surface of the expanded portion. Basal walls of zoecia strongly convex. Branches traversed by oblique joints, each zoecium being crossed by one joint near its proximal end and by another at the commencement of its expanded portion. Avicularia of two kinds, the smaller at the distal outer border of the zoecium, and a very large kind (present on only a few of the zoecia) arising from the inner border. Strong flexor zoecii muscles present, by which the branches are inflected. Ovicells very large. Bifurcation of type 6 (Pl. 16. fig. 6).

It can hardly be doubted that this very remarkable species, which was placed by Busk in a heterogeneous assemblage referred to *Cellularia*, deserves recognition as the type of a new genus. It was described recently, by the late Miss Alice Robertson (1921, Rec. Ind. Mus. xxii. p. 39), as *Kinetoskias arabianensis*, Roberts., n. sp.

*Euthyris*, Hincks, 1882, A. M. N. H. (5) x. p. 164.—Genosyntypes, *E. obtecta*, Hincks, n. sp., *Flustra bombycina*, Ellis and Solander (1786, p. 14) and *Carbasea episcopalis*, Busk (1852<sup>2</sup>, p. 52). *C. episcopalis* is the genotype of *Euthyroides*, Harmer, 1902. *F. bombycina* Ell. and Sol. (*nec* Busk; see *Onchoporella*), which appears to be at present unrecognizable, is the genotype of *Semiflustra*, D'Orbigny, 1852. *Euthyris obtecta* is thus left as the genotype of *Euthyris*, but if *F. bombycina* could be recognized it would probably become necessary to regard *Euthyris* as a synonym of *Semiflustra* (q. v.).

*Euthyroides*, Harmer, 1902, Q. J. M. S. xvi. p. 280.—Genotype, selected by the author, *Euthyroides episcopalis* (*Carbasea episcopalis*, Busk, 1852<sup>2</sup>, p. 52).

*Falcaria*, Oken, 1815, p. 91.—Genosyntypes, *Cellularia falcata* (Pallas, 1766, p. 76), s. *cornuta* (*Sertularia cornuta*, L., 1758, p. 810), *C. eburnea* (*S. eburnea*, L., 1758, p. 810) and *C. anguina* (*S. anguina*, L., 1758, p. 816); the first two referable to *Crisia*, and the third to *Aetea*, two genera introduced by Lamouroux in 1812. Gray (1848, p. 136) selected *Falcaria cornuta* as the genotype. Synonym of *Crisia*, Lamx., 1812, and pre-occupied in Lepidoptera by *Falcaria*, Haworth, 1809, Lepid. Britann. p. 152; for date of publication of which see Woodward, vol. ii. p. 804.

*Farcimia*, Fleming, 1828, p. 534.—Genotype (the only species), *Farcimia fistulosa* (*Eschara fistulosa*, L., 1758, p. 804). There is no justification for including *Nellia oculata*, Busk (see *Nellia*) in this genus, as has been done by Waters (1887, A. M. N. H. (5) xx. p. 92) and others. Synonym of *Cellaria*, Ell. and Sol. 1786.

\* εὐοπλος, well armed.

*Farcominaria*, Busk, 1852\*, p. 32.—Genotype (the only species), *Farcominaria aculeata*, Busk, n. sp.

*Filicella*, Searles Wood, 1844, A. M. N. H. xiii. p. 15.—Genotype (the only species), *Filicella anguinea*, S. Wood, n. sp., a Crag species, possibly the adnate part of a species of *Aetea*.

*Fistulana*, O. F. Müller, 1776, Zool. Dan. Prodr. p. 282.—In his *Corrigenda* (p. 282), Müller states that *Fistularia*, introduced in the same work, is to be changed to *Fistulana*, a course which was probably adopted because *Fistularia* was pre-occupied, in Pisces, by a Linnean genus (1758, p. 312) of the same name. *Fistularia* was introduced by Müller, without figures, on p. 254, with the genosyntypes *F. ramosa* (*Tubularia ramosa*, L., 1758, p. 804; 1767, p. 1302), *F. muscoides* (*T. muscoides*, L., 1767, p. 1302), *F. simplex*, *F. longicornis* and *F. multicornis*, Müll., n. spp. In 1780, Fabricius (Fauna Groenl. p. 441) uses *Fistulana* for *F. ramosa* and *F. muscoides*, quoting the diagnoses of Müller *verbatim*, in words identical with those of Linnæus, 1767. In 1789, Abildgaard (in Müller, Zool. Dan. iii. p. 15) describes and figures *F. multicornis*, quoting Müller's diagnosis, with additions.

Of Müller's species, the first two are Hydroids, while the diagnosis of *F. longicornis* suggests a Polychæte (Spionid). *F. simplex* may be a Ctenostome Polyzoon, while it seems probable, from Abildgaard's description and figures (pl. 90. figs. 1-3) that *F. multicornis* was also one of the Polyzoa. Smitt (1868, pp. 279, 280) suggests that it might be identical with *Aetea truncata*, Landsborough (see *Cercaripora*), but he points out, as an objection to this conclusion, that Müller had described the tentacles as 30 in number. This is not quite correct, as Müller described them as being "ultra viginti," and it was Abildgaard who stated that they were "ad triginta." In an earlier paper Smitt (1865, Öfv. K. Vet.-Akad. Förh. xxii. (1865), p. 13, pl. 3. fig. 4) had shown that *Aetea truncata* has 12 tentacles, and on this ground I think that *F. multicornis* cannot have been that species. Abildgaard's figures seem more likely to have been taken from a species of *Noellea*, Gosse (*Cylindrocium*, auctt.; see Harmer, 1915, Siboga Rep. Polyzoa. i. p. 52). *Fistulana* should be disregarded for Polyzoa. The same name was introduced in other groups by Bruguière (1789) and Lamarck (1799); see Sherborn, Index Animalium, i. 1902.

*Fistularia*, O. F. Müller, 1776, p. 254.—See *Fistulana*.

*Flabellaria*, Gray, 1848, pp. 106, 146.—Genosyntypes, *Sertularia spiralis*, Olivi, 1792 (Zool. Adriat. p. 291, pl. 6. figs. 2, a, A) and *Flustra setacea*, Fleming, 1828 (p. 536), referable to *Caberea*. *Bugula murrayana* was given as a synonym of Olivi's species; but the occurrence of this northern form in the Adriatic seems to be very unlikely, and Olivi's species ought probably to be placed elsewhere in *Bugula*. Gray's genus thus appears to be unnecessary. It may be remarked that *Flabellaria*, Lamarck, 1816, p. 342, is used for certain calcareous Algæ.



*Flabellaris*, Waters, 1898, J. L. S. xxvi. p. 672.—Based on several recent species, but with no clear indication which of them are to be included. *Menipea flabellum* (on which the generic name is obviously founded) is specially mentioned; and a description is given of *Membranipora roborata*, Hincks (1881, A. M. N. H. (5) viii. p. 128), which is referred to the genus. One of these two species might be selected as the genotype, but it seems unnecessary to do so, since the species mentioned on pp. 672, 673 of Waters' paper, in addition to those referred to by him, as given in one of his earlier papers (1897, J. L. S. xxvi. p. 2), can all be placed in other genera which antedate *Flabellaris*.

*Flabellina*, Levinson, 1902, Vid. Medd. naturh. Foren. Copenhagen, p. 21.—An emendation of *Flabellaris*, Waters, perhaps suggested because of the resemblance of this name to *Flabellaria*, Gray, 1848. The only species mentioned is *Flabellina roborata* (Hincks), 1881 (see *Flubellaris*); but the name is pre-occupied by *Flubellina*, Voigt, 1834, Das Thierreich, iii. p. 124, used for a Nudibranchiate Mollusc.

*Flustra*, Linnæus, 1761, Fauna Svecica, p. 539.—The history of this name has been given by Lang (1917, Geol. Mag., Dec. vi, vol. iv. p. 170), who shows that Linnæus deliberately altered his own genus *Eschara* (1758, p. 804) to *Flustra*, and that *Flustra foliacea*, Linn. (*Eschara foliacea*, 1758, p. 804) is the genotype of both genera. Although this course is not admissible under the Rules, I fully agree with Dr. Lang that it is in the highest degree desirable to suppress *Eschara* and to use *Flustra* in its accepted sense. It may be noted that Lamarck (1801, Syst. An. s. Vert. p. 383) accepted *Flustra*, with the genotype *Flustra foliacea*, L.

*Gemellaria*, Van Beneden, 1845, Nouv. Mém. Acad. Roy. Brux. xviii. p. 9.—Based on Savigny's name "Gémellaires," appearing at the foot of pl. xiii (referring to figs. 4<sup>1</sup>-4<sup>5</sup>) of the "Description de l'Égypte." Savigny's species was described by Audouin (1826, p. 243) as *Loricaria aegyptiaca*, without reference to the fact that *Loricaria* was used for a Fish by Linnæus (1758, p. 307), as pointed out by Fleming (1828, p. 541). Lamouroux (1827, p. 434) mentions *Gemellaria*, without any associated trivial name, but only to state that it is referable to *Loricaria*. Gregory (1893, Trans. Zool. Soc. xiii. p. 227) discusses the generic name, but de Blainville (1830, p. 425; see also 1834, p. 461), whom he quotes as the first author to mention the genus in a correct form, merely places *Gemellaria loriculata* in his synonymy of *Gemicellaria loriculata*, ascribing the combination wrongly to Savigny. The first use of the generic name which is completely in order appears to be that of Van Beneden, 1845, who describes *Gemellaria loriculata* (*Cellularia loriculata*, Pallas, 1766, p. 64 = *Sertularia loricata*, L., 1758, p. 815); and in this sense the genus has been used by the majority of recent writers. *Gemellaria* thus becomes a synonym of *Euratea* (q. v.). It is in any case desirable that it should drop out of use, since it is based on Savigny's "Gémellaires," and the species figured by this author is not congeneric with *S. loricata*, L. (See *Synnotum*.)

*Gemicellaria*, de Blainville, 1830, p. 425; see also 1834, p. 460.—Genosyntypes, *Gemicellaria loriculata* (see *Gemellaria*), among the synonyms of which

appears "*Gemellaria loriculata*, Savigny," a combination which was used neither by Savigny nor by Audouin; and *G. bursaria* (*Sertularia bursaria*, L., 1758, p. 814). These two species are respectively the genotypes of *Eucratea*, Lamx. 1812, and *Epistomia*, Fleming, 1828. *Gemicellaria*, which was an alteration of the genus proposed by Savigny, "sous le nom de *Gemellaria*" (really "Gémellaires"), thus becomes synonymous with two genera of earlier introduction.

*Halophila*, Gray, 1843, p. 292.—Genotype (the only species), *Halophila johnstonæ*, Gray, n. sp. (thus written, although frequently modified later, even by Gray himself, to *johnstoniæ*). If this species is referred to *Bugula*, as I think is proper, *Halophila* becomes a synonym of that genus.

*Heterocella*, Canu, 1907, Ann. Paléont. ii. p. 70 (sep. p. 14).—Genotype, selected by the author, *Heterocella fragilis* (*Vincularia fragilis*, DeFrance, 1829, Dict. Sci. Nat. lviii. p. 214). See also de Blainville, 1834, p. 454.

*Heteroflustra*, Levinsen, 1909, pp. 124, 125.—A very unsatisfactory genus, proposed for those species of *Flustra*, auctt., which have not been placed in other genera, and "must provisionally be characterized mainly in a negative way." This appears to mean that all species not belonging to *Flustra* (s. str.), *Sarsiflustra*, *Kenella*, *Retiflustra*, and *Spiralaria* (genera recognized by Levinsen, p. 88), together with other genera such as *Carbasa*, *Chariella*, etc. (not considered by him), are to be placed in this provisional genus, which has no validity until it is more definitely characterized.

*Hiantopora*, MacGillivray, 1887, Tr. Proc. R. Soc. Vict. xxiii. p. 208.—Genotype (the only species), *Hiantopora ferox* (*Lepralia ferox*, MacGillivray, 1869, *Ibid.* ix. p. 132).

*Himantozoum*\*, n. gen.—Genotype, *Himantozoum mirabile* (*Bugula mirabilis*, Busk, 1881, Q. J. M. S. xxi. p. 12; 1884, p. 39).

I propose this genus for Sect. α of *Bugula*, as given by Busk, 1884, p. 37, with the following diagnosis:—

Zoarium stalked, the stalk composed of rootlets and prolonged into an attaching tuft of rootlets. Zoecia biserial to multiserial, the biserial branches composed of asymmetrical zoecia, between which are intercalated, in the pluriserial branches, one or more rows of median zoecia, which are symmetrical and some of which produce eggs. The ovicells are vestigial, and the egg, which is of large size, develops in the body-cavity of the fertile zoecium. Opesia occupying all or most of the front, an operculum being distinguishable. Zoecia overlapping their predecessors on the basal surface, their proximal ends strongly forked. Avicularia unstalked, attached to the proximal ends of the zoecia, those of the lateral and median rows more or less unlike.

The differentiation of median, symmetrical, fertile zoecia, as well as the characters of the avicularia, are striking features of this genus. In addition to the genotype, the following species may be included:—*Bugula leontodon*, Busk (1884, p. 39), *B. sinuosa*, Busk (1884, p. 39), *B. margaritifera*, Busk

\* *imás*, a strap, in allusion to the strap-shaped branches.

(1884, p. 41) and *B. sinuosa*, Busk, var. *variabilis*, Kluge (1914, p. 632). Most of the species are from abyssal depths, the shallowest record being that of Busk, 80–150 fathoms, for *B. sinuosa*.

The statements in the diagnosis referring to the eggs are based on the examination of Siboga material. *B. versicolor*, a member of Busk's Sect. *a* (1884, pp. 37, 38), differs from the other three species in certain points which appear to be important, and I do not feel justified in placing it in *Himantozoum*, although I am unable to make any other suggestion. The most important of its characters are the large endozoecial ovicells, the unforked proximal ends of the zoecia, which barely overlap their predecessors, and the absence of avicularia.

*Hoplitella*, Levinsen, 1909, pp. 135, 136.—Genotype (the only species), *Hoplitella armata* (*Carbasea armata*, Busk, 1852<sup>2</sup>, p. 50).

*Huxleya*, Dyster, 1858, Q. J. M. S. vi. p. 260.—Genotype (the only species), *Huxleya fragilis*, Dyst., n. sp.

*Jubella*, Jullien, 1882, Bull. Soc. Zool. Franco, vii. p. 519.—Genotype (the only species), *Jubella enucleata*, Jull., n. sp., described as being near *Cuberea*, but differing from it by the absence of vibracula.

*Kenella*, Levinsen, 1909, p. 124.—Genotype (the only species), *Kenella biseriata* (*Flustra biseriata*, Busk, 1884, p. 54).

*Kinetoskias*, Danielssen, 1868, Forh. Vid.-Selsk. Christiania, Aar 1867, p. 23.—Genosyntypes, *K. arborescens* and *K. smithi*, Dan., n. spp. In their detailed account, Koren and Danielssen (1877, Faun. Litt. Norv. Pt. 3, pp. 104, 109) describe the same two species, the latter as *K. smittii*, but without comment on the altered spelling. There can be no doubt that this species was named after Prof. Smitt, and the form *smithi* should be considered a printer's error. *K. arborescens* is not a completely typical member of the genus, as the stalk is very short and the avicularia are more *Bugula*-like than usual. I propose accordingly to regard *Kinetoskias smittii* as the genotype.

*Loricaria*, Lamouroux, 1821, p. 7.—Genosyntypes, *L. europæa* and *L. americana*, Lamx., n. spp., both synonymous with *Eucratea loricata*, L. (q. v.). Pre-occupied by *Loricaria*, L. (Pisces), as pointed out by Fleming, 1828, p. 541. See *Gemellaria* and *Eucratea*.

*Loricula*, Templeton, 1836, Loudon's Mag. Nat. Hist. ix. p. 469.—This genus is usually attributed to Cuvier, who used it (1830, Règne An. Nouv. Éd. iii. p. 303) merely as "Les Loricules," proposing it for *Sertularia loricata*, L. (1758, p. 815), on the ground that "Loricaires" Lamx. (see *Loricaria*) was pre-occupied for Fishes. The genus was used in a correct form by Templeton, for *Loricula loricata*; and, later, by Voigt, 1843, Das Thierreich, vi. p. 248, in the same combination. It is synonymous with *Eucratea*, Lamx. 1812, with the same genotype, but it is pre-occupied by *Loricula*, Curtis, 1833, Ent. Mag. i. p. 197, for Hemiptera.

*Maplestonia*, MacGillivray, 1885, Tr. Proc. R. Soc. Vict. xxi. p. 92.—Genotype (the only species), *Maplestonia cirrata*, MacG., n. sp.

*Melicerita*.—The introduction of this genus by Milne Edwards (1836, A. S. N. Zool. (2) vi. p. 347), with only one species given merely as "*Mélicérîte de Charlesworth*," was not strictly in order. Searles Wood (1844; see *Ulidium*) quotes this as *Melicerita charlesworthii*, which was thus regularized, and became the genotype. His simultaneous introduction of *Ulidium*, with the same genotype, was unnecessary. In the A. S. N. (3) xvii., dated 1852, but probably published later, D'Orbigny refers to the species as *M. charlesworthii*.

*Meliceritina*, Ehrenberg, 1839, Phys. Abh. Akad. Wiss. Berlin, J. 1838, Tab. ii.—Proposed to replace *Melicerita*, which "*ist nicht sprachgemäss*." This emendation need not be accepted.

*Membranicellaria*, Levinsen, 1902, Vid. Medd. naturh. Foren. Copenhagen, 1902, p. 22 n.—Introduced for *Melicerita dubia*, Busk (1884, p. 97) and a number of Cretaceous species, which are indicated. Genotype, now selected, *Membranicellaria dubia* (*Melicerita dubia*, Busk). Levinsen subsequently (1909, p. 207) described *M. dubia*, from part of Busk's original material, but he gives *M. dubia*, Busk, as a doubtful synonym. His reason for inserting a query is not apparent, but if it should prove that two species were included in Busk's material the form described by Busk would be the genotype, as no other was indicated in Levinsen's original account.

*Menipea*, Lamouroux. 1812, p. 183.—Genosyntypes, *Cellaria cirrata*, Ellis and Solander (1786, p. 29), quoted by Lamouroux as *cirrata*, and *C. flabellum*, Ell. and Sol. (1786, p. 28). Genolotype, *Menipea cirrata*: see Schweigger, 1819, Tab. 8: 1820, p. 428. The reasons given by Marcus (1922, p. 11) for regarding *M. cirrata* as a synonym of *Cellularia crispa*, Pallas (1706, p. 71) seem to me sufficient. Pallas gave the locality as "*Oceanus Orientalis*," but on p. 72 he states that it was found with a *Fucus* qualified by the adjective "*capensis*," which presumably meant the Cape of Good Hope, as explicitly stated in the German Edition (1787, i. p. 107) of Pallas' work. Seba's figure (Thesaurus, iii. Pl. 101, No. 8) is hardly demonstrative, as it is stated to be by Marcus, but it may have referred to the species which was later described by Pallas, who gives this reference. The correct name of the genotype appears to be *Menipea crispa* (Pall.). Waters' selection (1897, J. L. S. xxvi. p. 2) of *M. buskii*, Wyv. Thoms. (see under *Emma*, in Sect. V.) is obviously invalidated by the fact that this species was not included by Lamouroux.

*Mononota*, Pieper, 1881.—See *Synnotum*.

*Monsella*, Canu, 1900, Bull. Soc. Géol. France (3) xxviii. p. 437.—Genotype, selected by the author, *Monsella eocena* (*Planicellaria eocena*, Meunier and Pergens, 1886, "*Les Bryozoaires du Système Montien (Éocène Inférieur)*," Louvain, privately printed, p. 7). Canu gives figures of this species, copied from Meunier and Pergens.

*Naresia*, Wyville Thomson, 1873, Nature, vii. p. 388; see also Humbert, 1874, J. de Zool. iii. p. 134 and Wyville Thomson, 1877, "*The Voyage of the*

Challenger," "The Atlantic," i. pp. 144, 142, 193, fig. on p. 143.—Genotype (the only species), *Naroesia cyathus*, Wyv. Thoms., n. sp. Synonym of *Kinetoskias*, Danielssen, 1868.

*Nellia*, Busk, 1852<sup>2</sup>, p. 18.—Genosyntypes, *Nellia oculata*, Busk, nom. nov. (*Salicornaria dichotoma*, Busk, 1852<sup>1</sup>, p. 367, nec *S. dichotoma*, Schweigger, 1819, Tab. 8; 1820, p. 428) and *N. simplex*, Busk, nom. nov. 1852<sup>2</sup>, p. 19 (*S. marginata*, Busk, 1852<sup>1</sup>, p. 367). Genoelectotype, *Nellia oculata*; see Canu, 1900, Bull. Soc. Géol. France (3) xxviii. p. 382. It seems moderately certain that *N. oculata* is a synonym of *Cellaria tenella*, Lamarck, 1816, p. 135; and the correct name of the genotype would thus be *Nellia tenella* (Lamk.).

*Notamia*, Fleming, 1828, p. 541.—Proposed, to replace *Loricaria* (q. v.), pre-occupied, for *Cellularia loriculata*, Pallas (1766, p. 64) (*Sertularia loricata*, L., 1758, p. 815) and *S. bursaria*, L. (1758, p. 814), but immediately qualified by the statement that *N. bursaria* is the type of a new genus, *Epistomia* (q. v.). The genotype is thus *Notamia loricata*, and the genus becomes a synonym of *Euratea*, Lamx. 1812 (q. v.). The loss of *Notamia*, in Polyzoa, would in any case have been inevitable, as the name was pre-occupied by *Notamia*, Rafinesque (1819, J. de Physique, etc., lxxxix. p. 153), introduced for a species described as a "Polype" and also as belonging to the Fam. Sipunculidæ, but with a terminal anus. See also *Gemellaria*.

*Notopites*, n. gen.—See p. 348.

*Onchoporella*, Busk, 1884, p. 103.—Genotype, *Carbasa bombycina*, Busk, 1852<sup>2</sup>, p. 52. Busk's species was not identical with *Flustra bombycina*, Ell. and Sol. (see *Euthyris*), and it thus appears necessary to propose a new name for *C. bombycina*, Busk. I suggest, therefore, that the genotype should be known as *Onchoporella buskii*, n. sp. I consider that Busk indicated his own *C. bombycina* as the genotype, by placing it alone under the generic heading, although he stated in a footnote (p. 104) that *Scruparia diaphana*, Busk, is a second species of *Onchoporella*. He here made a curious mistake, as it appears, on consulting the reference he gives (1860, Q. J. M. S. viii. p. 281, pl. 31. fig. 1), that he was deceived by the fact that fig. 1 does not occur as the first species on the Plate. It is clear, from the description and figures, that Busk meant to refer to fig. 2, which comes first on the Plate, and that the second species he intended to place in *Onchoporella* was *Carbasa ligulata*, described by him on p. 282 of his 1860 paper.

*Ornithopora*, D'Orbigny, 1852, A. S. N. (3) xvi. p. 312; 1852, P. F. T. C. p. 321.—Genotype (the only species), *Ornithopora avicularia* (*Sertularia avicularia* (pars), L., 1758, p. 809; *Cellularia avicularia*, Pallas, 1766, p. 68). This species is also the genotype of *Bugulina*, Gray, 1848; and the genus is a synonym of *Bugula*, Oken, 1815.

*Ornithoporina*, D'Orbigny, 1852, A. S. N. (3) xvi. pp. 312, 313 (*Ornithoorina*, errorim, on p. 312); 1852, P. F. T. C. p. 322.—In the A. S. N. D'Orbigny mentions only one species, *O. avicularia*, which should accordingly be regarded as the genotype. His citation of Ellis (1756, French Ed., p. 119, pl. 38. fig. 7) shows, however, that the species intended was probably *Avicularia*

*flabellata*, Gray, 1848, p. 106 (see *Avicularia*); and the correct name of the genotype is thus *Ornithoporus flabellata* (Thomps., MSS.) (Gray). In the second work cited D'Orbigny includes two other species as well. Synonym of *Avicularia*, Gray, 1848 (with the same genotype) and of *Bugula*, Oken, 1815.

*Petalostegus*, Levinsen, 1909, pp. 97, 114.—Genotype (the only species), *Petalostegus bicornis* (*Catenaria bicornis*, Busk, 1884, p. 14).

*Planicellaria*, D'Orbigny, 1852, A. S. N. (3) xvi. pp. 333, 338; P. F. T. C. pp. 26, 36, 181.—Genosyntypes, *P. oculata* and *P. fenestrata*, two fossil species, apparently belonging to different genera.

*Poricellaria*, D'Orbigny, 1852, A. S. N. (3) xvi. p. 338; 1854, P. F. T. C., p. 1106.—Genotype, selected by the author, *Poricellaria alata*, D'Orb., n. sp. Canu, 1907, Ann. Paléont. ii. p. 142 (sep. p. 38) regards *Diplodidymia*, Reuss, 1869, as a synonym of this genus; and he describes and figures a specimen which he refers to *D. alata* (D'Orb.).

*Retiflustra*, Levinson, 1909, pp. 124, 125, 414.—Genosyntypes, *R. schönaui*, Lev., n. sp., *Carbasea cribriformis*, Busk, 1852<sup>2</sup>, p. 51 (*Retepora cornea*, Busk, 1852<sup>1</sup>, p. 380) and *Flustra reticulum*, Hincks, 1882, A. M. N. H. (5) x. p. 163. Genotype, now selected, *Retiflustra cornea* (Busk).

*Rhabdozoum*, Hincks, 1882, A. M. N. H. (5) x. p. 160.—Genotype (the only species), *Rhabdozoum wilsoni*, Hincks, n. sp.

*Saccocydra*, Billard, 1914, 2<sup>e</sup> Exp. Antarct. Franç., Hydroides, p. 5.—Genotype (the only species), *Saccocydra problematica*, Billard, n. sp. Prof. Billard recently wrote to me informing me that he had ascertained this genus, described as a Hydroid, to be a synonym of *Barentsia*. There is no doubt, from his figures, that this conclusion is correct, and that *Saccocydra* is to be regarded as one of the Eutoprocta, and as a synonym of *Barentsia*, Hincks, 1880, A. M. N. H. (5) vi. p. 285. I publish this note at Prof. Billard's request.

*Salicornaria*, Schweigger, 1819, Tab. 8; 1820, p. 428.—This genus is usually attributed to Cuvier, 1817 (Règne An. iv. p. 75), who introduced it, in the form "Salicorniaires," for *Cellularia salicornia* (Pallas, 1866, p. 61), and three other species referable to *Tubucellaria* and *Menipea*. Schweigger seems to have been the first to use the form *Salicornaria*, while he may be considered to have selected the genotype by including only one species, *S. dichotoma* (*Cellularia salicornia*, Pall.). If *Cellaria* (q. v.) is accepted, *Salicornaria* becomes a synonym of that genus.

*Salicornia*, de Blainville, 1830, p. 419; see also 1834, p. 455.—De Blainville gives this as *Salicornia*, Cuv., although Cuvier did not use it in this form, and he includes two species, *Cellularia salicornia*, Pall. (see *Salicornaria*) and *Cellaria salicornioides*, Lamouroux (1816, p. 127, but not in Cuvier's list). *Salicornia* is merely another form of *Salicornaria*.

*Salicorniaria*, Schinz, 1825, Das Thierreich, iv. p. 155.—Another variant of the same name, the species included being those of Cuvier's original list (see *Salicornaria*), with some additional synonyms. The genus is used in the same form by Templeton (1836, Loudon's Mag. Nat. Hist. ix. p. 469).

- Salpingia*, Coppin, 1848, A. M. N. H. (2) ii. p. 273; see also Gray, 1848, p. 149.—Genotype (the only species), *Salpingia hassallii*, Copp., n. sp. Synonym of *Aetea*, Lamouroux, 1812.
- Sarsiflustra*, Jullien and Calvet, 1903, Rés. Camp. Sci. Prince de Monaco, xxiii. pp. 43, 126.—Genotype (the only species), *Sarsiflustra abyssicola* (*Flustra abyssicola* (M. Sars, MSS.), G. O. Sars, 1872, Christiania Univ. Progr. 1st half-year, 1869, p. 19).
- Scruparia*, Oken, 1815, p. 90.—Based on 9 species, one of which (*Cellularia repens*, presumably = *Sertularia repens*, Ellis and Solander, 1786, p. 52) is a Hydroid. The others are Polyzoa, corresponding with four modern genera. The first species mentioned, and the only one in which a trivial name is definitely associated with *Scruparia*, is *Scruparia chelata* (*Sertularia chelata*, L., 1758, p. 816). This was the only species included in *Scuparia* (errore), Gray, 1848, p. 132, and in *Scruparia*, Busk, 1852<sup>2</sup>, p. 28; in the latter case with a new diagnosis. *Scruparia chelata* should thus be regarded as the genotype. Hincks' later proposal (1880, p. 21) to make his own *S. clavata* the genotype is inadmissible, as this species is not included in Oken's original list. Verrill, 1880 (Proc. U. S. Nat. Mus. ii. 1879, p. 190) chose *S. reptans* [*Scrupocellaria*] as the genotype, but although in Oken's list, this species has no claims if those of *S. chelata* are established.
- Scrupocellaria*, Van Beneden, 1845, Nouv. Mém. Acad. Roy. Brux. xviii. p. 26.—Genotype (the only species), *Scrupocellaria scruposa* (*Sertularia scruposa*, L., 1758, p. 815).
- Scuparia*, Gray, 1848, p. 132.—This seems to have been a misquotation of *Scruparia* (q. v.).
- Scupocellaria*, Gray, 1848, p. 111.—A similar mistake for *Scrupocellaria* (q. v.).
- Selbia*, Gray, 1843, p. 292.—Genotype (the only species), *Selbia zelandica*, Gray, n. sp. Busk (1852<sup>2</sup>, pp. 37, 38) cites Gray's species as a synonym of *Caberea* (*Crisia*) *boryi*, Audouin (1826, p. 242): and even if not identical with Audouin's species, *Selbia*, of which no generic diagnosis was given, must be regarded as a synonym of *Caberea* (q. v.).
- Semiflustra*, D'Orbigny, 1852, A. S. N. (3) xvi. p. 317; 1852, P. F. T. C. p. 326.—Genotype, *Semiflustra bombycina* (*Flustra bombycina*, Ellis and Solander, 1786, p. 14), which is the only species mentioned in the "Annales des Sciences Naturelles." In the second work cited two other species are also included. *Curbasca bombycina*, Busk, 1852<sup>2</sup>, p. 52, is a distinct species (see *Onchoporella*). *Euthyris*, Hincks, 1882, A. M. N. H. (5) x. p. 164, may perhaps be regarded as a synonym of *Semiflustra* (see *Euthyris*).
- Spiralaria*, Busk, 1861, Q. J. M. S. (n. s.) i. p. 153.—Genotype, *Spiralaria florea*, Busk, n. sp.
- Spiralis*, Levensen, 1909, p. 408 (Explanation of Pl. 19. fig. 10 a).—A mistake for *Spiralaria*, as shown by p. 125.

*Stirparia*, Goldstein, 1880, Q. J. Mier. Soc. Viet. Proc. i. p. 75.—Genotype (the only species), *Stirparia annulata* (*Bicellaria annulata*, Maplestone, 1879, *t. cit.*, p. 19). The generic name is pre-occupied, for Ponnatulacea, by Leuckart, 1841, Zool. Bruchstücke, ii. p. 122; and I propose that it be replaced by *Stirpariella* (nom. nov.), with the genotype *Stirpariella annulata* (Mapl.).

*Stirpariella*, nom. nov.—See *Stirparia*.

*Stolonella*, Hincks, 1883, A. M. N. H. (5) xi. p. 197.—Genotype (the only species), *Stolonella clausa*, Hincks, n. sp.

*Synnota*, Pieper, 1881.—See *Synnotum*.

*Synnotum*, Pieper, 1881, Neunte Jahresb. Westfäl. Provinzial-Ver. pro 1880, p. 47.—Pieper suggested the alternative names *Mononota* and *Synnota* for a single new species, *Gemellaria* (?) *avicularis*. *Synnota* was adopted, but amended to *Synnotum*, presumably on etymological grounds, by Hincks, 1886 (A. M. N. H. (5) xvii. p. 255); and I think this change in spelling may be accepted. Waters (1897, J. L. S. xxvi. p. 15) pointed out that *S. aviculare* is probably a synonym of *Loricaria ægyptiaca*, Audouin, 1826, p. 243; and I have satisfied myself that this conclusion is correct. The name of the genotype should thus be *Synnotum ægyptiacum* (Aud.). It does not seem to have occurred to other authors that this species cannot be placed in the same genus as *Eucratea loricata* (Linn.). See *Eucratea* and *Gemellaria*.

*Ternicellaria*, D'Orbigny, 1851, P. F. T. C. pp. 40, 47; see also 1852, A. S. N. (3) xvi. p. 330.—Genotype (the only species), *Ternicellaria aculeata* (*Bicellaria* (*Tricellaria* on pl. 2) *aculeata*, D'Orb., 1839–1846, Voy. Amér. Mérid. v. 4, p. 8). Synonym of *Tricellaria*.

*Tricellaria*, Fleming, 1828, p. 540.—Genotype (the only species). *Tricellaria ternata* (*Cellaria ternata*, Ellis and Solander, 1786, p. 30).

*Utidium*, Searles Wood, 1844, A. M. N. H. xiii. p. 17.—Genotype (the only species), *Utidium charlesworthii* (*Melicerita charlesworthii*, Milne Edwards). The principal reasons given for its introduction are that *Melicerita* is etymologically incorrect, *Meliceritina* is objectionable, and names similar to *Melicerita* have been used in other groups. Synonym of *Melicerita*; see also *Meliceritina*.

*Unicellaria*, de Blainville, 1830, p. 425; see also 1834, p. 461.—Genosyntypes, *Sertularia chelata*, L. (as described by Ellis, 1756, Hist. Nat. Cor. French Ed. p. 57), *S. cornuta*, L., 1758 (p. 810), *Eucratea appendiculata*, Lamouroux, 1821 (p. 8), and *Lafoea lafoeyi*, de Blainville, nom. nov. for *Lafoea cornuta*, Lamouroux, 1821 (p. 8). The first of these species is referable to *Scruparia*, Oken, 1815; the second and third to *Crista*, Lamouroux, 1812; and the fourth appears to be a Hydroid.

*Watersia*, Levinsen, 1909, pp. 94, 99.—Genotype (the only species), *Watersia militaris* (*Flustra militaris*, Waters, 1887, A. M. N. H. (5) xx. p. 93).



## III. INTERNAL AVICULARIA.

Levinson (1909, p. 139, pl. 2. figs. 7*b*, *d*, *e*, *g*, *j*, *k*) has described the occasional replacement of an ordinary frontal avicularium, in *Menipea roborata*, by an avicularium which grows into the body-cavity; and in one of his letters quoted in Sect. V. (p. 336) he refers to the presence of internal avicularia in *M. marionensis*. He makes no comment on this extraordinary occurrence; but however improbable it may seem, both on morphological and on physiological grounds, there is no doubt of the accuracy of the description. I have found these internal avicularia, not only in the two species indicated by Levinson, but also in certain other species of the same genus.

The internal avicularia of *M. marionensis* are represented in three of my figures. Pl. 19. fig. 44, a basal view, shows one of these structures (*i. av.*) in each of the zoœcia D and E. The avicularium is a more or less cylindrical structure situated on the inner side of the frontal wall, and projecting basally into the body-cavity. The palatal surface is on the basal side, there is a normal beaked rostrum, with which is connected an acute, triangular mandible. The material is not in the best condition, and it has the appearance of having been allowed to dry. The polypides are, however, perfectly recognisable, and there seems to be clear evidence that the mandible opens and closes in the body-cavity, and in actual contact with the tissues of the polypide. The arrangement seems an inconvenient one, and I can suggest no explanation of its purpose. There is no evidence whatever that the avicularium lies in a cavity invaginated from the frontal side, and I cannot escape from the conclusion that the mandible actually moves in the body-cavity. Four of these internal avicularia are shown, in basal view, in Pl. 17. fig. 22, in the zoœcia C, D, E, and K. The base of the cylindrical avicularium, *i. av.* (Pl. 19. fig. 43), is not raised above the general level of the frontal wall, and from it originate the occlusor muscles, which are seen in frontal view, of the mandible. The avicularium has in fact an inverted position, and has been developed on the inner side of the wall of the zoœcium, instead of on its outer side.

The account given by Levinson of the internal avicularia of *Menipea roborata* is not easy to understand; and a renewed study of these remarkable structures was required. There is no doubt that, as stated by Levinson, the internal avicularium replaces an ordinary frontal avicularium. I do not find them always present, as he states, when an external avicularium is absent, and I have not found them in the marginal rows. They may usually be found without difficulty in some of the zoœcia of the submarginal rows, and occasionally in other zoœcia further removed from the margin. They seem to be always wanting on the distal side of an ovicell, where two external avicularia are constantly present, directed obliquely distally, and thus reversed

in their direction as compared with the avicularia not related to an ovicell ;— again in accordance with Levinsen's description.

The internal avicularium is longer than would be inferred from Levinsen's account. Its proximal end is in the same position as that of an external avicularium. The side view (Pl. 18. fig. 29) shows, in each of two zoecia, a pair of avicularia lying side by side. While one of them (*f.av.*) rises normally on the frontal side of the zoecium, the other (*i.av.*) runs distally and basally below the cryptocyst, the avicularium being long and sub-cylindrical, and terminating in a beaked rostrum, with an opesia subdivided by the projection into it of two calcareous teeth (see Levinsen, pl. 2. fig. 7*k*). In a frontal view (Pl. 18. fig. 30) the distal end of the internal avicularium (*i.av.*) is seen through the opesia, and its proximal end (*p.*) forms a slightly convex calcareous film, which is partly crossed by the triangular proximal end of the cryptocyst (*cr.*). This overgrowth by the cryptocyst does not occur in the external avicularia, which grow frontally from their base.

Levinson did not discover internal avicularia in *M. ligulata* and *M. spicata*, two species which were associated by MacGillivray with *M. roborata* in his genus *Craspedozoum* (see Sect. II.). I have found them in both these species, as well as in *M. rectifera*, n. sp. (see Sect. V.) and in *M. triseriata*, Busk. Their occurrence in undoubted species of *Menipea* is of special interest, as indicating that *Craspedozoum* should probably be merged in that genus.

The internal avicularia do not seem to be common in *M. ligulata*, but I have found them, as shown in Pl. 18. fig. 33, in one or two zoecia. They resemble those of *M. roborata*, but they appear to be less asymmetrical in position.

In *M. spicata* (figs. 32, 35) the internal avicularia are considerably smaller than in the other two species. They lie closely attached to one of the lateral walls of the zoecium, and do not reach its opesia (fig. 35). In side view (fig. 32) they are seen to pass nearly vertically downwards into the body-cavity. The internal avicularia of *M. rectifera* (fig. 36) resemble those of *M. spicata*.

In *M. triseriata* (Pl. 19. figs. 41, 42) the internal avicularium is broad and short, its distal end being just visible, through the opesia, in frontal view (fig. 42). It will be seen from these figures, as well as from one or two of those illustrating other species, that a considerable proportion of the internal avicularia found occur in the more proximal of the two zoecia formed when a longitudinal row is doubled.

The species in which I have found internal avicularia may all be placed in *Menipea*, s. str., as understood in Sect. V.; and they constitute a definite evidence of affinity in a group of species which can be placed together for other reasons. It seems probable that these remarkable structures will be found in other species of the same genus, though I have failed to find them at present in any but the ones which have been mentioned above.

## IV. METHODS OF BIFURCATION OF THE COLONY.

The "Cellularine" series of Cheilostomatous Polyzoa, which takes its name from the genus *Cellularia* (see Sect. II.), consists of numerous genera and species in which the zoecium has a membranous frontal wall and the colony has an erect, branching habit. The character of the frontal wall places them in Levinsen's Sub-order *Anasca* (1909, p. 91). The Cellularine habit of growth is closely paralleled, however, in members of the Sub-order *Ascophora*, in which the frontal wall is calcareous and a compensation-sac is present (cf. Harmer, 1902, ref. on p. 295). The genus *Catenicella* and its allies may be mentioned in this connection; but none of the Ascophorous genera are here considered.

The Anascous branching forms are usually placed, in systematic treatises, near the commencement of the Cheilostomatous series; and it has often been at least tacitly assumed that they represent a low stage in the evolution of the Cheilostomata. This view seems to me erroneous; and the highly evolved nature of this assemblage is indicated by the characters of their heterozoecia, a term introduced by Levinsen (Vid. Medd. Naturh. Foren. Copenhagen, 1902, p. 3) to include the avicularia and vibracula. The avicularium reaches the summit of its development in such Cellularine genera as *Bugula* and *Cornucopina*, while the vibraculum is highly specialized in *Caberea*, belonging to the same assemblage. The assumption that the branching habit is in any sense primitive appears to me fundamentally wrong. It is no doubt true that the Cellularine species are less adapted for preservation as fossils than the encrusting forms; but, making every allowance for this consideration, the Palæontological evidence points to the encrusting habit as the more primitive; and already in the Cretaceous Period, large numbers of encrusting Cheilostomes, of a primitive type in other respects, are known.

Not only are there these reasons for viewing with suspicion the claims of the Cellularine genera to be regarded as representing an early stage in evolution, but the study of their mode of branching leads readily to the conclusion that the erect colony is a lamina which has been more or less subdivided. It may be noticed that the majority of Cellularine species consist entirely of branches having two surfaces sharply differentiated. The basal surface of the branch shows merely the "backs" of the individual zoecia, all of which have their orifices on the opposite or frontal surface. There is thus no difficulty in regarding the typical Cellularine colony as a unilaminar sheet of zoecia, divided by more or less radial slits into narrow branches, which in the majority of species are built up of two longitudinal series of zoecia, alternating on the two sides of the branch. It might appear logical to regard the biserial condition as representing the last stage in this process, and thus to suppose that when biserial and multiserial branches occur in closely related species, the multiserial condition should in all cases

be regarded as the more primitive. I am not sure that this is always the case, and I think it is at least possible that a multiserial branch may in some cases have been derived secondarily from a preceding biserial condition. I do not consider it necessary to discuss this question in the present paper, in which I desire to point out, however, that the extent to which the splitting of the original lamina has taken place differs in various genera and species; and that the study of the actual facts of the bifurcation of the branches may be of great assistance in systematic work. So far as I am aware, there has been no previous comparative account of this subject, although the importance of the mode of branching has not been overlooked by other writers. I may refer especially to the account given by Davenport (1891, Bull. Mus. Comp. Zool. Harvard, xxii. p. 41) of the branching of *Bugula*, and to two papers by Waters (1897, J. Linn. Soc. xxvi. p. 2; 1913, Proc. Zool. Soc. p. 473), dealing with the mode of bifurcation in *Scrupocellaria* and *Menipea*. These papers record important facts, but they do not exhaust the subject. Davenport is concerned with the general laws of branching, and he does not attempt to show how his results can be applied to classification. In his 1913 paper Waters divides *Menipea* into several groups, based on differences in the mode of branching; but I think he has not been altogether successful in his conclusions. Waters (1913) defines a group "C," for instance, which he supposes to include species having a common type of bifurcation; but he places in it *Menipea patagonica* and *Bugulopsis peachii*, two species which, according to my own results, differ essentially in their mode of bifurcation.

In studying the bifurcation, particularly in the Family Scrupocellariidae, it is necessary to devote special attention to the formation of the chitinous joints with which many species are provided. In the majority of cases, each of the branches is jointed at its base, in such a way that the actual bifurcating point is immediately succeeded by a joint at the origin of each branch. In some cases, only one of the branches is thus jointed; an arrangement which may give rise to a sympodial form of stem, unilateral when the joints all occur on the same side, or bilateral when they are formed alternately on the two sides. The joint is developed in a manner which is remarkably constant in the most diverse members of the calcareous Polyzoa; occurring in fundamentally the same way in Cyclostomata (*Crisia*) and in a variety of Cheilostomata, which seem to have no close connection with one another. The process has been described by various authors, among whom I may mention Waters (1881, Q. J. Geol. Soc. xxxvii. p. 320; 1887, Ann. Mag. Nat. Hist. (5) xx. pp. 89, 92; 1897, J. Linn. Soc. xxvi. p. 2; 1913, Proc. Zool. Soc. p. 472); Pergens (1890, Bull. Soc. Belge Géol. iii. p. 313); and Lomas (1889, Proc. Liverpool Biol. Soc. iii. p. 219). The joint is formed across one or more zoecia, the calcareous walls of which are at first complete and continuous. A chitinous lining is developed on the inner side of the calcareous wall and in close contact with it (*cf.* Pergens, text-fig. 8, on

p. 314), in the form of a cylindrical tube, rather longer than the future joint, and open at both ends. An annular zone of the calcareous wall is then absorbed, at the middle of the chitinous tube, which is left as the sole connection between the distal part of the zoecium and the parent-internode. It thus follows that the jointed zoecium partakes in the formation of two internodes; the greater part of it usually lying in the proximal end of the daughter-internode, while the part on the proximal side of the chitinous joint is immersed in the parent-internode. The polypide commonly passes through the jointed region of the zoecium, not only in the early stage, before the absorption of the calcareous annulus, but through the chitinous tube even after the completion of the joint, and in fact throughout the whole period of its own life. The proximal segment of the jointed zoecium has often been described as a "special chamber" of the parent-internode, by authors who have not fully appreciated its morphological significance.

In certain cases, as in species of *Scrupocellaria* and in *Poricellaria* (*Diplo-didymia*), further strength is afforded to the joint by the development of additional tubes of chitin, each formed on the inner side of its predecessor and somewhat longer than it. A considerable number of these tubes may be formed, and the whole chitinous complex thus acquires a considerable thickness, showing at each end a series of rings of diminishing diameter in passing from the outer to the inner surface of the tube. This arrangement, which may be described as a system of tubes "en échelon," is indicated by Claparède (1870, *Zeitschr. wiss. Zool.* xxi. pl. 9. fig. 1 C), and his figure also shows the circular, transverse furrows of the annular thickenings of the calcareous wall with which the edges of the successive chitinous tubes are firmly united. This arrangement, which is most noticeable in the more robust species of *Scrupocellaria*, appears to be a mechanical arrangement admirably adapted to give the greatest strength at the middle of the joint, and to allow the entire stem the flexibility which is required in order to obviate fracture of the delicate branches.

The bifurcation of a biserial branch takes place by the doubling of the number of zoecia, and generally in such a way that two successive, alternating zoecia of opposite side of the parent-internode are each followed by two distal successors, instead of by a single successor as in parts where the internode is merely elongating without dividing. For the purpose of comparison I have adopted a uniform notation for the zoecia concerned in the bifurcation, as may be seen by reference to figs. 1-18. The more proximal of the two zoecia which prepare the way for the bifurcation is distinguished as A, and the more distal zoecium, on the other side of the branch, as B. C and D, on the outer sides of the arms of the Y-shaped bifurcation, may be regarded as the direct successors of A and B respectively; and it will be seen that they agree closely with their predecessors in form, differing from them only by diverging from one another to an extent sufficient to allow

two other zoëcia to be intercalated between them. These two zoëcia are denoted E and F; E being derived from A and lying on the inner side of C; and F being derived from B and lying on the inner side of D. E is usually in close relation with the axil of the bifurcation, and for this reason I term it the axillary zoëcium. It may be the proximal inner zoëcium of one of the branches and it is succeeded by G, the second inner zoëcium. F and H are the corresponding members of the other branch.

A careful study of various Cellularine genera, with particular reference to the relations of the zoëcia above enumerated (and in some cases of one or two additional zoëcia) has led me to the conclusion that the mode of bifurcation may be used as an important generic or specific character. I do not overlook the danger of relying exclusively on a single character, but the use I make of the bifurcation seems to be justified by finding that species thus assorted appear, on the evidence of other characters as well, to form natural groups. It appears to me probable that during the evolution of these genera particular methods of bifurcation were adopted at an early stage, and can be recognized, with modifications, in most if not in all of the species which constitute the genera. It must be added that in most of the species here considered the proximal end of the distal zoëcium of a longitudinal row overlaps its predecessor on its basal side. The diagrammatic figures are all representations of basal views, and the distal ends of the zoëcia are thus hidden by the proximal ends of their successors. The zoëcium A always lies to the right of the figure; and, in species in which A and B alternate, A typically lies on that side of the parent-internode which is external in relation to the preceding bifurcation. It thus follows that if the branches E C G and F D H were followed further to the points where new bifurcations occurred, the "A" zoëcium of each of these would be found on the outer side. The right hand bifurcation would be a repetition of the bifurcation actually figured, and the left hand bifurcation would be its looking-glass image, A lying on the left or outer side. *Didymozoom* forms an exception to this rule, as the intercalation of a median ovicell-bearing zoëcium takes place by a division of the inner row of a biserial branch into two rows.

Before bifurcation occurs, the zoëcia of opposite sides of the branch are in lateral contact with one another, and are connected by rosette-plates or communication-pores. In *Bugula* and some of its allies a peculiar modification of this relation is found at the bifurcations (Pl. 16. figs. 3-5). Before becoming completely disjoined, the two branches remain as a rule united with one another by a special communication, formed in the axil by two of the lower members of the branches. The connecting process (c. p.) is formed in several different ways, which are remarkably constant within the limits of a species, which may thus be distinguished from others with which it might be confused. In only one or two species I have found, however, that the more proximal bifurcations of a colony may belong to one type, and the more

distal ones to another. This is the case, for instance, in a colony of *Bicellarina alderi*, in which two successive types are represented; but, so far as my observations go, this is exceptional. It is well known, however, that the proximal end of a colony may show characters regarded as juvenile, as compared with the more differentiated distal parts; and even if it should be found that differences in the mode of bifurcation occur at opposite ends of the colony, in other species, it will not, I think, affect the correctness of the statement that each species of *Bugula* has a practically constant method of bifurcation, in its fully developed condition. It may be added, finally, that the arrangement assumed is dependent, in the main, on the extent to which the inner zoecia remain in lateral contact with one another, or, in other words, on the distance to which the split forming the bifurcation extends towards the zoecia A and B.

The position of the rootlets, with regard to the bifurcations, has previously been recognized as a character of importance, particularly by Waters (1897, 1913, cited on p. 321). In the series including *Menipea* and its allies, these structures are given off from a pore-chamber which projects into the body-cavity, sometimes on the distal side of the jointed region (fig. 15), and sometimes on its proximal side (figs. 9-11). The difference may appear a slight one, but the general flexibility of the colony must be affected by the position of the rootlets. It seems probable that, when a joint has been evolved, the relation of the rootlets to it would not be easily altered during subsequent modifications of the species. Thus one series of species, represented by *Menipea* and *Notoplites*, may be supposed to have started with their rootlets on the distal sides of the joints, and at the proximal ends of the internodes; and to have retained these relations during their later evolution. *Tricellaria* may be similarly supposed to have originated from a condition in which the rootlets were on the proximal sides of the joints and at the distal ends of the internodes.

Levinson (1909, p. 132 n.) has stated that vestigial vibracula may be recognized in the pore-chambers of the rootlets of *Tricellaria ternata*. I think this view is correct, and in fig. 11 I have shown structures which admit of this interpretation in *T. peachii*, on the proximal segments of the zoecia C and D. In *Scrupocellaria* each zoecium is typically provided with a vibraculum, which lies on the basal surface of the branch, usually near its external border. The vibraculum belongs to the proximal end of the zoecium, although it is in close relation with the external or marginal avicularium of the preceding zoecium of the same longitudinal row. The vibraculum is constantly provided, in this genus, with a chamber, cut off by calcareous walls from the cavity which contains its muscles, and this chamber gives origin to a rootlet, in the more proximal members of the colony at least; although in many of the other vibracula the rootlet is merely represented by an oval fenestra in the outer wall of the rootlet-chamber, corresponding exactly with

the fenestra occurring in a vibraculum which actually develops a rootlet. I cannot agree with Levinson's statement (1909, p. 134) that the rootlet-chamber is not thus cut off in *Scrupocellaria*. In *Tricellaria peachii* (fig. 11) the structure from which the rootlet originates is a chamber cut off by a wall from a more distally placed portion which shows a slight longitudinal groove, apparently representing the rostral groove which receives the seta of a normal vibraculum. I regard the structure in question as a vestigial vibraculum, situated in its proper place at the proximal end of a zoecium and on its basal surface. The rootlet-chambers thus situated are doubtless the rootlets produced by "a definite dorso-lateral chamber situated just above the lateral avicularium," mentioned by Miss Robertson (1905, Univ. California Publ., Zool. ii. p. 250) in "*Menipea*" (*Tricellaria*). As pointed out by the same author, the rootlets given off by these chambers may pass distally and form the tendril-like structures known to occur in *Tricellaria*. The tendrils are not always formed in this way, however; as I find that in *Emma tricellata*, Busk, one of these structures may replace a branch at a bifurcation. I believe this to occur by the suppression of the proximal segment of F or G at a bifurcation, as in fig. 13, and by the hypertrophy of the chitinous tube which would otherwise have formed a joint, unaccompanied by the production of the calcareous parts constituting a zoecium. In other cases, as in fig. 12, a rootlet is developed from the outer side of a zoecium which is not concerned in a bifurcation. The pore-chamber of the rootlet is still in the proper place for a vibraculum, at the proximal end of a zoecium; and although greatly reduced may still represent that structure.

The rootlets which do not become tendrils pass proximally, sometimes along the basal surface, but in many cases along the lateral margins of the branches. The formation of lateral bundles of parallel rootlets is specially characteristic of *Amastigia*, *Notoplites*, and *Menipea*.

Type 1 (Pl. 16. fig. 1).—The zoecia occur in pairs, and not alternately on the two sides of the branch. A and B are thus at the same level, and the split separating the two branches reaches their distal ends. E, C and F, D thus form symmetrical pairs, E and F remaining in contact with one another, at their proximal ends, on the basal side of A and B.—*Didymozoum*. (The arrangement is slightly modified in an internode which has become triserial distally by the development of an ovicell.)

Type 2 (fig. 2).—Bifurcation occurs before a doubling of the number of zoecia takes place, the proximal end of each branch being thus uniserial. C remains in contact with the inner lobe of the proximal fork of D; and the doubling of the number of zoecia takes place at the distal ends of C and D, or of one of their successors if more than a single uniserial zoecium occurs at the proximal end of the branch.—*Stirpariella*, sp. ('Siboga' Collection).



Type 3 (fig. 3).—The split extends nearly to the proximal end of the axillary zoecium, E, which is accordingly free, on its inner side, for the greater part of its length. E gives off a connecting process (c.p.) to meet the proximal end of F. In the species figured, each of the pairs E, C and F, D has a single fork, at the proximal end, divided by the common septal wall in such a way that each of the four zoecia has only a half fork, instead of a complete fork as in the other zoecia.—*Bugula johnstonæ* (Gray), 1843, and other species of this genus.

Type 4 (fig. 4).—The split does not extend proximally so far as in type 3, not more than half the axillary zoecium (E) being free on its inner side. The connecting process (c.p.) is given off by F, and joins the inner lobe of the fork of G, which crosses the basal side of E.—Species of *Bugula*, e. g., *B. scaphoides*, Kirkp., 1890, A. M. N. H. (6) v. p. 18, and *Dicellariella*, and most of the species of *Stirpariella*, e. g., *S. zanzibariensis*, Waters, 1913, P. Z. S. p. 469.

Type 5 (fig. 5).—The axillary zoecium is almost completely immersed in the parent-internode, the split only reaching its distal end. The connecting process (c.p.) is given off by G and joins the inner lobe of the fork of H.—Species of *Bugula*, e. g., *B. dentata* (Lamx.), 1816, p. 135, and of *Stirpariella*, e. g., *S. caraibica*, Levinsen, 1909, p. 104.

Type 6 (fig. 6).—Although F is in contact with B, it appears to be derived from E, which it meets near the middle of the length of the latter. The connection between the proximal ends of the inner zoecia of the branches is formed by the independent junction of F and G with E. The proximal ends of the zoecia are not bifurcate. Oblique joints, indicated by dotted lines and of a type common in *Bugula*, traverse the zoecia.—*Euoplouszum cirratum* (Busk), 1884, p. 17.

Type 7 (fig. 7).—Resembles type 6 in the relation of G and F to E, but is peculiar in other respects. The axillary zoecium (E), which gives rise to F and G, passes into the proximal end of the branch on the side opposite to A, a relation which has not been found in any other type. B takes no part in the doubling of the number of zoecia, the proximal ends of which are not bifurcate.—*Kinetoskias cyathus* and all the other species (4) examined.

In the following types (8–18) the position of the chitinous joints is of importance.

Type 8 (fig. 8).—The proximal segments of F and G are in contact on the basal side of E, and are shorter than the corresponding parts of C and D; the joints traversing F and G near their proximal ends, and passing much more distally through C and D. In the species figured (*Scrupocellaria ferox*, Busk, 1852), the joint traverses the middle of the opesia, which is represented by dotted lines, of each of the outer zoecia C and D. In certain other

species of the genus each joint passes across the proximal end of the opesia of the outer zoecium; and in others, particularly in those with elongated zoecia, it passes entirely on the proximal side of the opesia of C and D.—*Scrupocellaria*, all species. *Himantozoum* may be considered to belong to this type, with which it agrees except that it is unjointed.

Type 9 (fig. 9).—The proximal segments of F and G are not in contact, and are shorter than the corresponding parts of C and D; the joints traversing CG and DF respectively. A rootlet-chamber occurs on the proximal segment of C or D, or of both, and the rootlet is thus given off on the proximal side of the joint.—*Tricellaria*, spp.

Type 10 (fig. 10).—The proximal segments of F and G are separated by the whole width of E, and the two branches come off at different levels, that on the side of A being the more proximally situated. Internodes commonly composed of three zoecia, C and D then taking on the character of A and B zoecia in the next internode.—*Tricellaria*, spp. (Figured specimen, *T. occidentalis* var. *dilatata*, Ortmann, 1889, p. 21.)

Type 11 (fig. 11).—Except in the fact that the proximal segments of F and G are in contact, this agrees with type 9.—*Tricellaria peachii* (Busk).

Type 12 (fig. 12).—Readily derivable from type 10 by the suppression of the proximal segments of F and G, the internode thus consisting of a single zoecium at its proximal end, connected with its predecessor by a single chitinous joint.—*Tricellaria aculeata*, D'Orb.

Type 13 (fig. 13).—A modification agreeing with type 12, occurring in *Emma cyathus*. The zoecia C and D take on the character of A and B zoecia at their distal ends.

Type 14 (fig. 14).—Internodes composed of three zoecia and, like the zoecia, very short. A slight modification of type 9.—*Emma*, spp.

Type 15 (fig. 15).—Proximal segments of F and G in contact, much longer than the corresponding parts of J and K. The joints are on the distal sides of C and D, and traverse the zoecia FJ and GK. The joints are situated at some distance from the axil, instead of being on the same level with it, and do not traverse the opesia of any zoecium. Rootlets given off on the distal sides of the joints.—*Notoplites*. A modification represented, in the same genus, in the 'Siboga' Collection results from the suppression of one of the joints of the bifurcation.

Type 16 (Pl. 17, fig. 16).—The axillary zoecium is free on both sides distally. The zoecia F and G are not in contact with one another, but each is connected with one side of E at a point marked by the presence of a conspicuous rosette-plate (*r.p.*).—*Cornucopina*, all species examined. The zoecia are very long, and a constriction partially separates a small proximal section from the main part of the zoecium.

Type 17 (fig. 17).—Proximal segments of F and G in contact (rarely separated), longer than the corresponding parts of J and K. The joints are on the distal sides of C and D, lying hardly in advance of the axil, and they traverse the zoecia FJ and GK, passing through the opesia of F and G, the two inner zoecia. Rootlets given off on the distal sides of the joints.—*Menipea*.

Type 18 (fig. 18).—The internode becomes triserial by the development of a median row of two or more zoecia. The distal member of the median row ( $E^2$  in the figured specimen) behaves as an axillary zoecium. Bifurcation in other respects as in type 17.—*Menipea* (triserial species).

Type 19 (fig. 19).—Part of a sympodial colony of *Menipea spicata*, only one of the branches being jointed at each bifurcation.

Type 20 (fig. 20).—Agreeing with type 8 except for the intercalation of a median series of zoecia in the internode.—*Amastigia kirkpatricki* (Lev., MSS.), n. sp.

#### V. CHARACTERS OF CERTAIN GENERA AND SPECIES OF SCRUPOCELLARIIDÆ.

##### Family SCRUPOCELLARIIDÆ.

Cellulariidae, Hincks, 1880, p. cxxxvii; Busk, 1884, p. xxii; MacGillivray, 1887, Trans. Proc. R. Soc. Vict. xxiii. p. 199; *et auctt.*

Scrupocellariidae, Levensen, 1909, pp. 89, 130; Canu & Bassler, 1920, U.S. Nat. Mus., Bull. 106, p. 180.

A diagnosis, based on Levensen's study of the Family, has been given by Canu and Bassler, and this may be accepted with but few modifications. The Family consists of Anasceous Cheilostomata, of erect habit, usually much branched, and attached by rootlets. With rare exceptions the zoarium is unilaminar, and the branches are biserial in the majority of species. The branches are nearly always flexible, well-developed chitinous joints occurring in most cases. The opesia is large, and spines usually occur distally or at the sides of the orifice. A specially modified spine, the scutum or fornix, jointed at its base, projects horizontally over the opesia, being branched or broadened except in the region of its narrow stalk; but it may be completely wanting. The full equipment of heterozoecia consists of (1) an avicularium, or a pair of avicularia, on the frontal surface, typically on the proximal side of the opesia, and with the rostra directed proximally. The frontal avicularia on the distal side of an ovicell are commonly paired and directed distally; (2) a lateral or marginal avicularium at the outer distal corner of the zoecium; (3) a basal heterozoecium, which may be either an avicularium or a vibraculum, on the basal surface, at the proximal end of the zoecium, usually in contact with the lateral avicularium of the preceding zoecium. The heterozoecia are not jointed at their base, and any or all of them may

be wanting. The mandibles of the avicularia are invariably of the pointed type. The terminal wall of the zoecium is at first vertical, its origin from the basal wall straight or slightly curved, but then bends distally, in approaching the frontal surface; the proximal portion of each zoecium thus overlapping its predecessor on its basal side. The ovicells are hyperstomial, frequently completely contained in a depression on the frontal wall of the zoecium which succeeds the fertile zoecium, and not projecting beyond the general frontal level of the zoecia.

The scutum and the heterozoecia appear to be very capricious in their occurrence. In several of the genera one or more of these structures are present, on most of the zoecia, in certain species; while they are absent in other species which appear to be closely allied to those of the first series. I think the only interpretation which can be given of these facts is that all these structures are to be regarded as original possessions of the Family, and that their absence is to be attributed to loss.

Dr. W. D. Lang has come to a similar conclusion with regard to Cretaceous Cribrimorphs (1922, Cat. Foss. Bry. (Pol.) Brit. Mus. iv. pp. 3, 156, and elsewhere).

The extreme amount of loss is found in *Tricellaria peachii*, in which scutum and heterozoecia are completely wanting, if exception be made of the possibly vestigial vibraculum which has been described on p. 324. On the assumption that the heterozoecia are structures which give their possessors some advantage in the struggle for existence, it is very difficult to understand the frequency with which they disappear entirely; the species in which this takes place continuing to exist, apparently with undiminished efficiency.

Genera here considered :—

1. *Amastigia*, Busk.
2. *Menipea*, Lamouroux.
3. *Notoplites*, n. gen.
4. *Tricellaria*, Fleming.
5. *Emma*, Gray.
6. *Scrupocellaria*, Van Beneden.

[The genera *Canda* and *Caberea* are omitted.]

#### 1. AMASTIGIA, Busk.

*Amastigia*, Busk, 1852<sup>2</sup>, p. 40.

*Caberiella*, Levinson, 1908, pp. 134, 135.

*Andersonia*, Kluge, 1914, p. 617.

*Scrupocellaria* (pars) and *Menipea* (pars), auctt.

Zoarium usually unjointed, the branches in nearly all cases pluriserial. Frontal surface typically convex, so that the marginal zoecia face outwardly, the basal surface more or less flat, the zoecia of the median rows as a rule partially or completely excluded from it. Spines, scutum, frontal and marginal avicularia present or wanting. Basal heterozoecia typically

present, in the form of avicularia, occasionally vibraculoid, or of vibracula. Rootlets given off by the basal heterozoecia or from the sides of the marginal zoecia, passing proximally as marginal bundles down the colony and frequently extending round the axils of the bifurcations. Ovicells typically small, often with a frontal fénestra.

Distribution, circumpolar (Southern), reaching as far north as Victoria in shallow water and Valparaiso in deep water.

The characteristic features of this genus appear to be the pluriserial branches, which are usually more or less semi-cylindrical, with the zoecia opening on the curved surface; the tendency for the basal walls of some of the inner zoecia to be reduced; the occurrence of basal heterozoecia (sometimes wanting); and the arrangement of the rootlets in marginal bundles. The last character also occurs in *Menipea* and *Notoplites*. The genus is of special interest as demonstrating, better than any other, the intimate relation between avicularia and vibracula. Joints definitely associated with a bifurcation seldom occur, but there is reason to believe that even in "unjointed" species they may be formed secondarily, as fractures occurring at some point of an internode, the fracture being mended by the formation of chitinous connecting tubes formed externally to the zoecia and not as a modification of their own body-walls. It is not unlikely that I have included too many species in this genus, which may have to be further subdivided.

1. *AMASTIGIA NUDA*, Busk. (Pl. 17. figs. 21, 24, 25; Pl. 19. figs. 50, 51.)

*Amastigia nuda*, Busk, 1852<sup>4</sup>, p. 40, pl. 36. figs. 1-5. Tierra del Fuego.

" " (*pars*), MacGillivray, 1887, Trans. Proc. R. Soc. Vict. xxiii. p. 200. Victoria.

The interest of this remarkable species seems to have completely escaped recognition since the publication of Busk's original account. MacGillivray records it, on the authority of J. Bracebridge Wilson, from Victoria, and the record is confirmed by slides in the British Museum. Kluge (1914, p. 613) mentions the genus only to dismiss it.

The type-slide (Brit. Mus. 54.11.15.87), from material collected by Charles Darwin, shows some interesting peculiarities which were not noticed by Busk. The branches are at first biserial, and the zoecia of the two rows here meet one another, in a normal manner, in the middle line of the basal surface. They later become 3-serial, and then 5-serial, by the intercalation of three additional rows. A basal view of a 5-serial region shows the appearance indicated in Pl. 17. fig. 24. The greater part of the basal surface is formed by the marginal zoecia (1, 5), while the median (3) and submedian (2, 4) zoecia have only a restricted origin from this wall. The frontal surface is very convex, the middle region being much thicker than the sides, and the marginal zoecia face obliquely outwards. As shown in Busk's figs. 2, 8, there is a large, undivided scutum, rounded distally. A frontal avicularium may occur on the submedian zoecia, but there is usually a pair on those of

the median row, the rostrum directed obliquely proximally except on the distal side of an ovicell, where the direction is reversed, as in allied species. A characteristic feature of Busk's specimen is the occurrence of well-developed lateral avicularia on the marginal zoöcia. The most interesting point is the presence of basal avicularia, which give off rootlets running on the inner side of the lateral avicularia, as shown in Busk's figs. 4, 5. These have an acute rostrum, directed proximally, and they are rather longer than wide, but not vibraculoid. The spines are well developed, though thin; four occurring on the outer side of the marginal zoöcia and two, in addition to the scutum, on the inner side. Scutum (Pl. 19. fig. 50) with a cavity which is very narrow at its commencement but dilates towards the free edge. The other zoöcia have three spines on each side, one of them being a scutum on one side. In several of the marginal zoöcia the distal external spine, which is jointed at its base, is enormously elongated, being much longer than a zoöcium, and running straight distally, just on the outer side of the margin of the branch, and parallel with it. The thick walls of these enlarged spines appear to be entirely chitinous. The ovicells have a frontal fenestra.

In addition to the type-slide the British Museum possesses the following specimens which I refer to *A. nuda*:—

- 97.5.1.246. Port Phillip Heads, Victoria, J. Bracebridge Wilson.  
 97.5.1.266 and 267. Same locality and donor (labelled *Menipea funiculata*).  
 97.5.1.250. Port Phillip, Victoria, Miss E. C. Jelly (labelled *A. nuda*).  
 99.7.1.823. Australia, Busk Collection (labelled *A. nuda*).  
 87.12.9.68. Kerguelen, 'Challenger' Collection, Stat. 149 I., 45–127 fathoms.  
 Recorded by Busk (1884, p. 19) as *Menipea benemunita*.

97.5.1.266 and 267 agree with the type, and differ from the other Victorian specimens, by possessing conspicuous marginal avicularia. Some of their spines are considerably enlarged, notably the second and third marginal ones, and the spine on the distal side of the scutum. I have hesitated whether to consider them distinct from the other Victorian specimens, but I think it is safer to regard them as one species. Basal avicularia are plentiful in all, sometimes completely alternate on the two sides of the branch and sometimes, in the same colony, meeting one another in pairs (Pl. 17. fig. 25). The branches are at most 5-serial, and the number of spines and the frontal avicularia (fig. 21) agree with the corresponding parts of the type. It is noteworthy that ovicells occur in all five rows.

The 'Challenger' specimen from Kerguelen is of more slender habit than typical *A. benemunita*, and is 5-serial. Its scutum is smaller than in that species, and its spines are 4, 2+scutum, on the marginal zoöcia, and 3, 3 (one being a scutum) on the others. In all these respects, as in the characters of the marginal and frontal avicularia, it agrees with *A. nuda*, to which I refer it. If my determinations are correct, this species has a circumpolar distribution, from Tierra del Fuego to Kerguelen and Victoria.

On isolating the rows of zoecia, after boiling in Eau de Javelle, the method by which the zoecia of the median rows become partially separated from the basal surface becomes apparent. As shown by Pl. 19. fig. 51, the basal wall is very sinuous, the vertical diameter of the body-cavity being greatest on the distal side of the length of the zoecium, and smallest at the proximal end. The prominent part of the wall reaches the basal surface of the branch, while the indented proximal part is excluded from it, the lateral walls of the adjacent zoecia sending lobes across this part, nearly or quite meeting one another. The lozenges formed by the median zoecia on the basal wall are thus produced; and the arrangement will be more easily understood by referring to Pl. 17. fig. 27 (*A. rudis*), in which the complete lateral outline of the distal median zoecium is represented. It will be seen that the greatest prominence of the basal wall corresponds with the widest part of the zoecium, while the proximal region of the zoecium is narrower, and is either completely excluded from the basal wall or only meets it in a linear median region. I believe this to be the method universally adopted in this group of species, when the zoecia meet the basal wall partially.

2. *AMASTIGIA RUDIS* (Busk). (Pl. 17. figs. 26, 27; Pl. 19. figs. 49, 52.)

*Caberea rudis*, Busk, 1852<sup>1</sup> p. 377; 1852<sup>2</sup>, p. 38, pl. 40. figs. 1-3.

" " MacGillivray, 1887, Prodr. Vict., Dec. xiv. p. 137, pl. 136. figs. 1-1 b.

*Menipea marginata*, Hincks, 1884, A.M.N.H. (5) xiv. p. 276, pl. 9. figs. 1-1 d; 1893, *Ibid.* (6) xii. p. 143.

Branches 2-8-serial, coarser than in the preceding species, the zoecia larger in all their measurements. Frontal surface strongly convex, the marginal zoecia facing outwards. Basal surface flat or concave, the marginal zoecia often projecting strongly as a broad, convex, longitudinal band on each side, the region of the median rows depressed and concave. Marginal zoecium forming a disproportionate part of the basal surface, the others reaching the wall in regularly alternating lozenge-like areas, the proximal end of each of these zoecia being overlapped by the broad parts of those of contiguous rows, and excluded from the basal wall or meeting it in a linear region. Opesia longer than in *A. nuda*, the cryptocyst not quite so much developed. Spines more uniform in size than in *A. nuda*, those of the marginal zoecia 4, 1, the fourth external more nearly vertical than the others. Spines in the other zoecia 2, 2; the second of one side in the form of a scutum, which does not fill the opesia, its distal lobe pointed (Pl. 19. fig. 49), its cavity as in *A. nuda*. Frontal avicularia paired on some of the median rows, meeting in a median suture, their rostra directed as in the preceding species; those in relation with an ovicell distant from one another. Outer frontal avicularium suppressed on the marginal and often on the submarginal rows, where the inner avicularium is often enlarged. On the marginal zoecia the single frontal avicularium is commonly

gigantic (Pl. 17. fig. 26), with a strongly hooked rostrum, its articular condyles strong and spike-like, and the mandible triangular and pointed (as in the other avicularia), and with an incurved acuminate tip. Marginal avicularia wanting. Basal heterozoöcia in the form of curved vibracula (fig. 27), placed in alternating pairs, the tip of the rostrum of each vibraculum meeting the middle of its predecessor on the opposite side of the branch. Rootlets as in other species. Ovicells resembling those of *A. nuda*.

Described from specimens in the British Museum, including Busk's type (54.11.15.82).

The basal heterozoöcia of *A. rudis* (Pl. 17. fig. 27) are of the kind described by Levinsen (1909, p. 135) as "curved or angularly bent vibracula" in *A. benemunita*, as noticed under that species. Levinsen founded the genus *Caberiella* on this character, not recognizing the fact that *Menipea benemunita*, Busk, is referable to *Amastigia*. Vibracula of this type occur in profusion in *A. rudis*, varying in size but not in form. The rostral groove, in which the long seta is received, is very long. The occurrence of different types of basal heterozoöcia in *Amastigia nuda* and *A. rudis* indicates that these structures are in a plastic condition in the genus, assuming the form indifferently of avicularia and vibracula, or being completely absent.

In side view (Pl. 19. fig. 52) the zoöcia are very different from those of *A. nuda*, being larger in all their dimensions. The terminal wall is more vertical, and the proximal end of the zoöcium much deeper, the median zoöcia being more completely represented on the basal wall than in that species, a fact with which the smaller amount of sinuosity of the basal wall (Pl. 19. fig. 52) is associated. The lateral communication-plates, as in other species of *Amastigia* (as well as in *Menipea*), are two in number.

The basal view (Pl. 17. fig. 27) of a branch of *A. rudis* is very characteristic. The marginal zoöcia occupy a disproportionate amount of this wall, but the others, though here reduced, are not nearly as much so as in *A. nuda*. Each zoöcium is wide distally, where it meets the basal wall along its whole width. It becomes narrower proximally, as shown in the distal zoöcium of the median row; but the greater part of this region is excluded from the basal surface by the union or close approximation of the widened parts of the preceding zoöcia of the rows on either side of it. The basal walls of all the zoöcia except those of the marginal rows thus appear as a series of regularly alternating spindle-shaped figures. The basal vibracula, which are not drawn on the younger zoöcia, are another very characteristic feature of the species.

*A. rudis* differs from *A. nuda* in the larger number of series of zoöcia in its branches, in the smaller number of spines, in the distal lobe of the scutum which is usually pointed, in the character of the basal heterozoöcia, in the gigantic frontal avicularia of the marginal rows, and in the larger measurements of all of its parts.



3. *AMASTIGIA CRASSIMARGINATA* (Busk).

*Caberea crassimarginata*, Busk, 1884, p. 28, pl. 11. figs. 1-1 b. S.E. of Buenos Aires, 600 fathoms.

Rootlets running down the margins of the branches. Vibracula covering only a small part of the basal surface, and resembling those of *A. rudis*. Although this species is biserial the characters of its rootlets, vibracula and scutum are in agreement with those of other species which I refer to *Amastigia*. Waters (1913, Proc. Zool. Soc. p. 480) has suggested that it should be placed in *Canda*.

4. *AMASTIGIA BENEMUNITA* (Busk).

*Menipea benemunita*, Busk, 1884, p. 19, pl. 4. figs. 4, 4 a (specimens from Stations 303 (probably 308), 313, 314, 315 only). Straits of Magellan, W. of S. end of S. America, Falkland Is., 5-175 fathoms.

*Scrupocellaria benemunita*, Jullien, 1888. Miss. Sci. Cap Horn, vi. p. 60, pl. 8. figs. 1-3. S. of Cape Horn, 90 metres.

*Caberiella benemunita*, Levinson, 1909, p. 135, pl. 22. figs. 8 a, 8 b. 'Challenger' Exp., Stat. 313.

British Museum, 'Challenger' Collection, 87.12.9.69-73. The type-slide is 87.12.9.70, Stat. 313, E. end of the Straits of Magellan, 55 fathoms. Sir John Murray thought that a mistake was made in one of the records, and that Stat. 303 (slide 87.12.9.69) should have been Stat. 308, the depth of which was 175 fathoms, and the locality near the W. coast of the S. end of S. America.

This species has a close resemblance to *A. nuda*, and it is curious that Busk did not refer it to his own genus *Amastigia*. It can be distinguished from *A. nuda* by its much larger scutum, with a large, upturned, truncate, distal lobe, and by its flatter branches, which may be at least 7-serial, in which all the zoecia appear to meet the basal wall normally, although the width of the median zoecia, basally, is less than that of the marginal zoecia. The spines of the marginal zoecia are 3, 1+scutum. Marginal avicularia are minute and commonly wanting. Under *A. rudis* I have alluded to Levinson's account of the basal heterozoecia, which he found in a 'Challenger' specimen from Stat. 313. I have not found heterozoecia of this type in the British Museum slide (87.12.9.70) from this Station, and the specimen seems to have only a single basal heterozoecium closely resembling those of *A. nuda*. In 87.12.9.72, from Stat. 315, basal vibracula as described by Levinson occur; and they resemble those figured by me (Pl. 17. fig. 27) in *A. rudis*. The occurrence of two different types of basal heterozoecia in different specimens of what I think must certainly be referred to the same species is an interesting fact.

The 'Challenger' slide from Stat. 149, Kerguelen, referred to this species by Busk, appears to belong to *A. nuda*.

5. *AMASTIGIA FUNICULATA* (*MacGillivray*).

*Menipea funiculata*, MacGillivray, 1886, Trans. Proc. R. Soc. Vict. xxii. p. 128, pl. 1. figs. 8, 8a; 1889, Prodr. Zool. Vict., Dec. xviii. p. 285, pl. 177. figs. 6-6b. Victoria.

The British Museum possesses several Victorian specimens (87.12.10.38; 88.11.14.221, 241; 97.5.1, 247, 269) of this species. It resembles *A. nuda* in general appearance, but the frontal surfaces of the peripheral branches are flat, and all the zoëcia meet the basal wall normally. Some of the spines are long and thick, particularly the second of the outer group of three in the marginal zoëcia. The single inner spine and the third or proximal outer spine are short and thick, often crossing one another over the orifice of the zoëcium. The scutum is oval, with a simple cavity, and it fills most of the opesia. The branches are in the main triserial, sometimes 4-serial, and marginal avicularia occur, though not commonly; both these and the frontal avicularia being small. I have not found basal heterozoëcia. The branches do not form joints at the bifurcations, but although typically unjointed there seem to be indications of the occasional occurrence of secondarily formed joints. The more proximally placed branches may be narrow, with a very convex frontal surface.

6. *AMASTIGIA ABYSSICOLA* (*Kluge*).

*Scrupocellaria funiculata*, Waters, 1904, 'Belgica' Bryozoa, p. 23, pl. 8. figs. 1a, b. Antarctic, 2800 metres.

*Scrupocellaria abyssicola*, Kluge, 1914, p. 611. Antarctic, 2450 metres.

Kluge doubts Waters' determination, and has suggested a new name for the deep water Antarctic form observed by Waters and himself. Basal heterozoëcia not described.

7. *AMASTIGIA CABERIOIDES* (*Kluge*).

*Scrupocellaria caberiodes*, Kluge, 1914, p. 612, pl. xxvii. figs. 9, 10. Antarctic, 350-385 metres.

Unjointed, 2-4-serial. Scutum originating distally, not filling the opesia, oval or long and narrow, the stalk inserted into the distal end of its lamina. Marginal and frontal avicularia, the latter sometimes gigantic. Basal avicularia paired, directed obliquely proximally, the tip of the rostrum slightly vibraculoid. Median zoëcia much reduced basally. Kluge rejects his own suggestion that this species might be placed in *Amastigia*.

8. *AMASTIGIA KIRKPATRICKI* (*Levinson, MSS.*), n. sp. (Pl. 17. fig. 20; Pl. 19. figs. 46-48.)

*Menipea marionensis* (pars), Busk, 1884, p. 21, pl. 14. fig. 9 (specimens from Stat. 144 a, Marion Island, 60-75 fathoms, only).

Branches biserial, becoming triserial at a varying distance from the proximal end. Internodes usually of 3-6 pairs of zoëcia, with at least one

median zoëcium preceding the bifurcation, often with a row of 2-4 median zoëcia. Rootlets arising from the proximal members, mainly attached to the edges of the branches, some of them passing down the basal surface. Opesia oval, rather more than half the frontal length, with a moderate cryptocyst, extending completely round the opesia, and of practically equal width all round. Spines one external (rarely two) and one internal, at the distal end, the external spine placed rather more distally than the internal; occasionally more numerous (fig. 46), the figure probably representing a zoëcium in an early state of growth of a colony. Scutum wanting. Frontal avicularia single on most of the zoëcia, those of some of the median zoëcia enlarged or even gigantic (fig. 48); much raised, directed obliquely proximally, and situated on the inner side of the zoëcium, on the proximal side of the opesia, which they do not reach. Two frontal avicularia may be found on the axillary zoëcium. Marginal avicularia small, often absent. Vibracula large, on the inner side of the lateral zoëcia, placed nearly longitudinally. the rostrum or groove for the seta greatly prolonged beyond the main part of the vibraculum, and reaching the middle line of the branch; a single vibraculum in the axil of the bifurcation. Ovicells large, longer than wide, the frontal surface rather flat, becoming concave just distally to the rim of the orifice of the ovicell. The surface is imperforate, and the ectoëcium covers only a narrow part of the frontal surface. Bifurcation (fig. 20) as described below; both branches jointed at their base, the joint involving the proximal end of the opesia of the outer zoëcium.

Type-slide (Brit. Mus.), 87.12.9.97, 'Challenger' Coll., Stat. 144 a.

In his 'Challenger' Report, Busk described as *Menipea marionensis* specimens from the two following localities:—

Stat. 142, off Cape of Good Hope, 150 fathoms; Stat. 144 a, off Marion Island, 50-75 fathoms.

On Oct. 4, 1910, the late Mr. G. M. R. Levinson wrote to Mr. R. Kirkpatrick, at the British Museum, stating that a fragment of a 'Challenger' specimen of "*Menipea marionensis*," from Stat. 144 a, had come into his hands, through the Dundee Museum, and that it proved to be a *Caberea*. On Jan. 26, 1911, he wrote further, to the effect that he had described and figured the species from Stat. 144 a, as *Caberea kirkpatricki*; and, having examined material, from Stat. 142, which had been sent to him by Mr. Kirkpatrick, he had found that "the great plurality of the frontal avicularia are internal" in *M. marionensis*. In returning the material which had been lent to him, he added a label to the specimens from Stat. 144 a, as follows:—"Busk had wrongly named the specimen *M. marionensis*, the type of which is from Stat. 142, Cape of Good Hope."

Levinson died in 1914, and, although I have made every effort to satisfy myself on the subject, I have failed to find evidence that his results were published. It must be assumed that the description referred to in his letter

of Jan. 26, 1911, remained in MS. at the time of his death. Having examined the whole of the material from the two Stations, I can confirm all Levinsen's statements of fact quoted above, although I do not agree with him in placing the new species in *Caberea*. There is no doubt that Busk confused two species, and it is unfortunate that *marionensis* must be applied, as shown by his description, to a species from the Cape of Good Hope, not at present known to occur off Marion Island.

I have adopted Levinsen's MS. name *kirkpatricki* for the new species ; and I give below a new diagnosis of *Menipea marionensis*. The two species can readily be distinguished under a low magnification. In *Menipea marionensis* the joints are placed at some distance from the axil of the bifurcation, the ovicells are small and short, there are no vibracula, and none of the frontal avicularia are enlarged. In *Amastigia kirkpatricki* the joints are at the level of the axil, the ovicells are large and long, conspicuous basal vibracula are present, and the frontal avicularium of the axillary zoecium (or of the proximal median zoecium if more than one is present) is usually much larger than the others. This last feature is indicated in Busk's fig. 9 (Pl. 14.), which I suppose to have been drawn from a specimen obtained at Stat. 144a, and therefore to belong to *Amastigia kirkpatricki*. In describing a species obtained from more than one locality, it is always expedient to indicate the locality of the specimens figured ; and this omission, by Busk and others, gives rise to many difficulties.

With reference to Levinsen's proposal to place this species in *Caberea*, I think it desirable to exclude from this genus those species in which the rootlets pass down the margins of the branches instead of down the middle of the basal surface. I think that *C. rudis*, Busk, should be placed in *Amastigia*, and that *C. crassimarginata*, Busk, may be referred to the same genus. It must be admitted that *A. kirkpatricki* has a considerable claim to be included in *Scrupocellaria*, which it resembles in its mode of bifurcation (Pl. 17. fig. 20). The branches are well jointed at their commencement, but a median series of zoecia, usually commencing near the proximal end of the internode, is present, in opposition to what is found in typical *Scrupocellaria*. The first median zoecium ( $E^1$ ) originates from a zoecium ("A"), situated on the outer side of a branch with reference to the preceding bifurcation. It gives to a second ( $E^2$ ), which may be followed by others in a median row. The distal member of this series ( $E^3$  in fig. 20) behaves as an axillary zoecium.

*A. kirkpatricki* thus seems to unite the characters of more than one genus, which may be explained by the assumption that *Amastigia* represents, better than any other genus, the ancestral character of the Scrupocellariidae, and that its species show approaches in various directions to those of other genera. I have suggested above that the pluriserial condition was probably antecedent to the biserial condition ; and on this view *A. kirkpatricki* is a species which

has almost become biserial, while its basal heterozoezia have acquired the full vibracular form, so as closely to resemble those of *Scrupocellaria*. *A. kirkpatricki* from Marion Id., *A. gaussi* from the Antarctic, and *A. crassimarginata* from off Buenos Aires all come from localities within the range of *Amastigia* and apparently outside that of *Scrupocellaria*; and their distribution supports the conclusion I have come to on other grounds as to their generic position.

The vibraculum (fig. 47) possesses a rootlet-foramen of the usual kind, situated opposite the proximal end of the muscular mass and given off from a small chamber separated by a calcareous wall from the rest of the vibraculum. The figure shows what appears to be another rounded chamber on the distal side of the rootlet-chamber. In side view this is seen to be continuous with the main vibracular chamber, and it is really the foot by which the vibraculum is connected with the proximal end of its zoecium, a communication-pore occurring in the wall which separates it from the zoecium.

#### 9. *AMASTIGIA GAUSSI* (Kluge).

*Scrupocellaria gaussi*, Kluge, 1914, p. 609, pl. 27. figs. 3, 4. Antarctic.

Closely allied to *A. kirkpatricki*, and differing from it mainly in possessing a scutum, and in being 2-5-serial.

#### 10. *AMASTIGIA SOLIDA* (Kluge).

*Scrupocellaria solida*, Kluge, 1914, p. 611, pl. 27. figs. 7, 8. Antarctic, 350-385 metres.

Unjointed, 3-serial. Stalk of scutum connected with the middle of its lamina, which is lobed externally. Frontal avicularia occur, but marginal avicularia are not described. Basal avicularia paired, directed transversely inwards, the rostrum rather more vibraculoid than in the last species. Median zoecia reduced on the basal surface.

#### 11. *AMASTIGIA ANTARCTICA* (Kluge).

*Andersonia antarctica*, Kluge, 1914, p. 618, pl. 33. figs. 3, 4. Antarctic, 76-170 metres.

Unjointed, 6-8-serial. Scutum and spines wanting, the opesia with straight lateral margins. The marginal zoecia face outwards, and they form the whole of the basal surface. Frontal avicularia present. The lateral avicularia described appear to be morphologically basal avicularia, since they are placed on the proximal and not on the distal ends of the zoecia. They are large and are arranged alternately on the basal surface, the rostrum directed obliquely proximally and being linear distally. A rootlet-foramen is present, a structure which seems to decide the question that these are basal heterozoezia.

This species differs from the others described by Kluge in the absence of spines and scuta; and in these respects it has a considerable resemblance to

the *Craspedozoum* group of *Menipea*. Its reference to *Amastigia* seems to be indicated by its well developed basal heterozoecia and by the complete exclusion of all the zoecia except those of the marginal rows from the basal wall.

## 12. AMASTIGIA PATERIFORMIS (*Busk*).

*Menipea pateriformis*, Busk, 1884, p. 22, pl. 5. figs. 4, 4 a. Off Valparaíso. 2160 fathoms.

The type-specimen (Brit. Mus. 87.12.9.101) has not been satisfactorily described by Busk. It appears to be allied to *A. antarctica*, which it resembles in the absence of scutum and spines. It agrees with *Amastigia* in possessing basal heterozoecia, which may be regarded as avicularia, although the mandible is distally linear and rather long. The rostrum is directed obliquely proximally. The colony is apparently unjointed, the branch thick and semicylindrical, the marginal zoecia facing obliquely outwards; a median row of zoecia, or two submedian rows, occurring in parts of the colony. Rootlets in two lateral groups. Frontal avicularia stout and prominent, the mandibles broadly triangular proximally, becoming narrow distally. Ovicells large, and distinctly long and narrow.

## 2. MENIPEA, *Lamouroux*.

*Menipea*, Lamouroux, 1812, p. 183.

*Craspedozoum*, MacGillivray, 1886, Trans. Proc. R. Soc. Vict. xxii. p. 131.

*Flabellaris* (*pars*), Waters, 1898, J. Linn. Soc. xxvi. p. 672.

*Flabellina*, Levinsen, Vid. Medd. Naturh. Foren. Copenhagen, 1902, p. 21.

*Cellularia* (*pars*), Busk, *et auctt.*

Zoarium jointed (rarely unjointed): the joints, if present, traversing the opesia of each of the *inner* zoecia at a bifurcation (Types 17, 18. Pl. 17. figs. 17, 18). Branches biserial to pluriserial. Scutum wanting. Frontal and marginal avicularia present or wanting; basal heterozoecia found only in *M. rectifera*. In several species a frontal avicularium may grow inwards into the body-cavity, instead of occupying the position normal to these avicularia. Rootlets associated with a bifurcation originating on the distal side of the joint. The rootlets are nearly always in lateral bundles, as in *Amastigia* and *Notoplites*.

The genus *Menipea*, as usually understood, embraces a number of species which are apparently not nearly allied. I lay special stress, in re-defining the genus, on the fact that (in all the jointed species) the joint traverses the opesia of the *inner* zoecium, in each branch. This may happen in such a way that a portion of the opesia lies on each side of the joint (Pl. 17. fig. 17); or the proximal end of the opesia may lie in the region of the joint (fig. 18). The relation of the joint to the opesia is implied by Busk (1852<sup>3</sup>, p. 21) when he states that in *M. cirrata* one of the lower zoecia in the internode is more or less aborted.

The species here included in *Menipea* form a group with a considerable resemblance to one another in general *facies*. It will be observed that (No. 2 excepted) they are all Southern forms, and that none of the Northern species are included:—a result which has already been anticipated by Norman (1903, A. M. N. H. (7) xi. p. 578).

1. *MENIPEA CRISPA* (*Pall.*). (Pl. 17. fig. 17.)

*Cellularia crispa*, Pallas, 1766, p. 71.

*Cellaria cirrata*, Ellis and Solander, 1786, p. 20, pl. 4. figs. *d*, *D*. "East Indies."

*Menipea cirrata*, Busk, 1852<sup>2</sup>, p. 21, pl. 20. figs. 1, 2. S. Africa.

*Menipea crispa*, Marcus, 1922, p. 11.

Easily recognizable by the characteristic inflexion of the branches, described by Pallas and well represented in Ellis and Solander's fig. *d*, and by the very long, cylindrical frontal avicularia (Busk, fig. 1), situated on the proximal border of the opesia, which they overarch. There are typically six zoœcia in the internode, which commonly has a single, large lateral avicularium. Three strong, curved spines, jointed at the base, are commonly present on the outer side of the distal end of the zoœcium.

2. *MENIPEA FLABELLUM* (*Ell. and Sol.*).

*Cellaria flabellum* (*pars*), Ellis and Solander, 1786, p. 28, pl. 4. figs. *c*, *C*.

Ellis and Solander state that two distinct species are included in their account of *C. flabellum*, one from the Bahama Is. and the other from the E. Indies. From the description it would appear that the figured specimens are from the Bahamas, although they might quite well be taken to represent the South African form to which this name has usually been applied. Perhaps a mistake in the locality of the specimens was made in the original account; but in view of the uncertainty of the question I think it best to use the name given by Busk, as indicated in the next species, for the common S. African species. *M. flabellum*, Ell. and Sol. may be regarded as at present unrecognizable.

3. *MENIPEA ORNATA* (*Busk*).

?*Cellularia floccosa*, Pallas, 1766, p. 70.

*Cellularia ornata*, Busk, 1852<sup>2</sup>, p. 20, pl. 26. figs. 3, 4. Algoa Bay.

*Menipea flabellum*, Busk, 1884, p. 21. Simon's Bay, Cape of Good Hope.

" " Marcus, 1922, p. 13, figs. 7 *a-c*.

*Flabellaris flabellum*, Waters, 1898, J. L. S. xxvi, p. 672.

Internodes often increasing regularly in width from the proximal to the distal end, their lateral margins nearly straight; the number of constituent zoœcia reaching at least 13. Marginal avicularia and spines wanting. Frontal avicularia inconspicuous, not prominent, often confined to the zoœcia E, F, and G; when on F and G occurring on the part of the zoœcium on the proximal side of the joint, as shown in Busk's fig. 3.

4. *MENIPEA PATAGONICA*, Busk.

*Menipea patagonica*, Busk, 1852<sup>2</sup>, p. 22, pl. 23. fig. 1; pl. 25. figs. 1-3; pl. 26. figs. 1, 2. Falkland Is., Patagonia.

*Menipea patagonica*, Jullien, 1888, Miss. Sci. Cap Horn, vi. p. 71. Tierra del Fuego.  
*? Scrupocellaria patagonica*, Kluge, 1914, p. 615, text-fig. 4. Kerguelen.

Internodes commonly consisting of six zoecia. A single spine typically present on each side, or two on the outer side, distally. Marginal avicularia well developed, frontal avicularia small.

5. *MENIPEA MARIONENSIS*, Busk. (Pl. 17. fig. 22; Pl. 19. figs. 43-45.)

*Menipea marionensis* (pars), Busk, 1884, p. 21, pl. 4. figs. 3, 3a (specimens from Stat. 142, Cape of Good Hope, 150 fathoms, only).

Branches mainly biserial, the axillary zoecium sometimes preceded by a more proximal median zoecium. Internodes usually of 3-5 pairs of zoecia, in addition to the median zoecium or zoecia, but sometimes with a larger number, particularly in those with ovicells. Zoecia facing obliquely outwards, from a raised keel passing down the middle of the branch. Opesia nearly oval, but distinctly wider distally, the cryptocyst more developed proximally than elsewhere. Strong calcareous spines given off basally from the edge of the cryptocyst, in young zoecia, becoming more numerous with increased age, and some of them directed frontally. Spines usually two external and one internal, often one on each side, the external spine the more distal. Scutum wanting. Frontal avicularia single on most of the zoecia, the rostrum directed obliquely proximally; not quite reaching the opesia. Two symmetrically placed frontal avicularia may occur on the axillary zoecium, where two median zoecia are present. Frontal avicularia of the usual type may be replaced by internal avicularia (Pl. 17. fig. 22; Pl. 19. figs. 43, 44), situated in the body-cavity. Marginal avicularia moderate, constantly present. Vibracula and basal avicularia wanting. Ovicells very short, wider than long. At the bifurcation (fig. 22) both branches are jointed, the distal end of the parent-internode being prolonged beyond the axil like the base of a tuning-fork. The joints are thus at some distance from the axil and traverse the proximal end of the opesia of each inner zoecium. Zoecia F and G meeting in a long median suture on the basal side of E.

The material which was described by Busk as *M. marionensis* included two very distinct species, as has been explained above (p. 336), under *Amastipia kirkpatricki*. The 'Challenger' specimens (Brit. Mus.) referable to *M. marionensis* are four slides, 87.12.9.94, 95 and 99.7.1. 698, 699, all from Stat. 142; 87.12.9.94 being marked as the type.

In examining the spirit material of *Menipea triseriata* obtained by the 'Challenger' from Simon's Bay, Cape of Good Hope, I found a fragment of another species, the original of my figs. 22, 43, and 45 of this



species. Its determination was confirmed when I remounted in Canada balsam one of Busk's dry slides (99.7.1.698) of *M. marionensis* from Stat. 142. Fig. 44 has been drawn from Busk's slide thus treated.

The calcareous spines developed from the cryptocyst are one of the most striking features of a Canada balsam preparation of *Menipea marionensis*. They are relatively few in young zoecia, in which they are directed towards the basal surface (figs. 22, 43, 44). In the older zoecia (fig. 45) they are much more numerous, some of them being branched, and some of them being directed towards the frontal membrane. These spines appear to be of the same nature as the similar structures which have been described by Levinson (1909, p. 138, pl. ii. fig. 7, c-e) in *Menipea roborata*. As in other members of its family, each distal zoecium of *Menipea marionensis* overlaps its predecessor to a considerable extent on its basal surface, as indicated in fig. 22. In the older zoecium represented (fig. 45) *p* is the proximal wall of the distal zoecium, and the opesia has been restricted by the formation of a horizontal calcareous lamina, the free edge of which is in the form of a Gothic arch (*e*); while the opesia is further reduced by the enlargement of the proximal cryptocyst.

The remarkable internal avicularia of this species are described above, in Sect. III.

6. *MENIPEA TRISERIATA*, Busk. (Pl. 17. fig. 18; Pl. 19. figs. 40-42.)

? *Crisia elegans*, Lamouroux, 1821, p. 6, pl. 65. figs. 4-7. Cape of Good Hope.

*Menipea triseriata*, Busk, 1852<sup>1</sup>, p. 22, pl. 23. figs. 2-4. S. Africa.

" " Busk, 1884, p. 21. Cape of Good Hope.

" " Waters, 1898, J. L. S. xxvi. p. 672, pl. 48. fig. 12.

Internodes more or less triserial, composed of numerous zoecia. External spines 2, internal 2, on outer zoecia; 1, 1 on median zoecia. Cryptocyst strongly developed on the proximal side of the opesia, covered with minute tubercles, its free margin here strongly thickened, and usually produced into a strong median tooth which may be directed basally. Marginal avicularia on most of the zoecia. Frontal avicularia often two on the median zoecia, one of which may be replaced by an internal avicularium; reversed (the rostrum directed distally) on the distal side of an ovicell, an arrangement commonly found in this genus. The outer frontal avicularium is wanting on the marginal zoecia. Ovicells short, usually broader than long.

The British Museum possesses a number of slides, all from South Africa.

A specially interesting feature of this genus is the possession of internal avicularia (figs. 41, 42), which have been described above, under Sect. III.

7. *MENIPEA QUADRATA* (Busk).

*Cekularia quadrata*, Busk, 1884, p. 18, pl. 5. figs. 5-5 b. Kerguelen, Heard Island.

Internodes long and narrow, consisting of numerous zoecia. Spines and frontal avicularia wanting. Marginal avicularia small.

8. *MENIPEA FLAGELLIFERA*, Busk.

*Menipea flagellifera*, Busk, 1884, p. 21, pl. 4. figs. 1-1 b. Kerguelen, Marion Id., Straits of Magellan, W. of Falkland Is.

*Scrupocellaria flagellifera*, Kluge, 1914, p. 615, text-fig. 5. Kerguelen.

Internodes of moderate length. Usually a single external spine. Marginal avicularia large. Frontal heterozoecia vibraculoid.

The frontal heterozoecia of this species are so peculiar as to suggest the possibility that it should be placed in a new genus. I refer it to *Menipea* because it has the mode of bifurcation characteristic of the genus, the joints traversing the opesia of each inner zoecium. The frontal heterozoecia, which are constantly present, have the seta of a vibraculum, but they do not possess the rootlet-foramen which is always found in a basal heterozoecium, whether it is an avicularium or a vibraculum. In view of the fact that in *Amastigia* avicularia and vibracula are interchangeable on the basal surface, a corresponding plasticity may perhaps be conceded to *Menipea*. The structures in question replace the frontal avicularia of other species; and, in spite of the presence of a greatly elongated mandible, I think they may be regarded as avicularia.

9. *MENIPEA SPICATA* (MacGillivray). (Pl. 17. fig. 19; Pl. 18. figs. 32, 34, 35.)

*Craspedozoum spicatum*, MacGillivray, 1886, p. 132, pl. i. figs. 2, 2 a; 1889, Prodr. Zool. Vict., Dec. xviii. p. 283, pl. 177. figs. 3-3 b. Victoria.

Unilaminar. Internodes curved frontally, composed of numerous zoecia, biserial at their origin, becoming 4-serial distally. Bifurcation cymose, owing to the fact that only one of the branches is jointed; the ultimate branches being unilateral cymes and the larger stems being bilateral (fig. 19). While the lateral internodes give off a single branch, those of the larger stems give off two branches, one on each side. The proximal branch comes off near the commencement of the internode, and forms the commencement of a lateral branch. The distal branch is placed in the line of the main stem, of which it forms a segment, and the distal, unjointed termination of the parent-internode diverges from the stem, on the same side of it as the proximal branch. The mode of branching of *M. spicata* does not seem to have been previously noticed, but a similar suppression of one of the joints occurs also in the allied genera *Notoplites* and *Tricellaria*. The affinity of *M. spicata* to the other species which I place in *Menipea* is shown by the fact that the joint traverses the opesia of an inner zoecium.

*M. spicata* has two well-developed spines on the outer side of the marginal zoecia and one on the inner side; and one spine on each side of the median zoecia. The cryptocyst is strongly developed on the proximal side of the opesia, and calcareous spines project into the body-cavity from the lateral walls, as in *M. roborata*. The ordinary frontal avicularia do not occur on all

the zoëcia, but when present they are large and prominent. They are very asymmetrical, the rostrum much elevated, and situated at the outer side of the zoëcium, indicating that the avicularium is one of the pair found in other species, its direction being as required by this hypothesis. Internal avicularia (figs. 32, 35) occur, always in zoëcia which do not succeed an ovicell, and, as noticed on p. 319, they are concealed by the proximal cryptocyst, in frontal view. They are considerably smaller than in *M. roborata*, and they lie close to one side of the zoëcium, being directed almost vertically towards the basal surface. Ovicells occur only on the two median rows, and two strong calcareous thickenings of the frontal wall converge distally, uniting with one another to form a strong recurved spike projecting in the middle line beyond the ovicell (fig. 34). The basal walls of the median zoëcia are considerably constricted near the middle (fig. 35).

This and the next two species were placed in *Craspedozoum* by MacGillivray (1886, Trans. Proc. R. Soc. Vict. xxii. p. 131), who instituted this genus for their reception. They are all provided with the lateral bundles of rootlets which usually occur in *Menipea*. The pore-chamber for the rootlet (fig. 35) is situated in the usual place, at the proximal end of a marginal zoëcium, and it probably represents a vestigial basal heterozoëcium. It is inconspicuous in *M. spicata*, in which there are no blister-like pore-chambers on the terminal walls, at their insertion into the basal wall.

The British Museum possesses several slides of Victorian specimens (88.11.14.97, 298; 97.5.1.459, 460; 83.10.15.46).

#### 10. *MENIPEA* *LIGULATA* (MacGillivray). (Pl. 18. figs. 31, 33.)

*Craspedozoum ligulatum*, MacGillivray, 1886, p. 132, pl. 1. figs. 3 3a; 1889, Prodr.

Zool. Vict., Dec. xviii. p. 283, pl. 177. figs. 1, 1b, 2. Victoria.

*Flabellaris roborata*, var. *ligulata*, Waters, 1898, J. Linn. Soc. xxvi. p. 672.

*Menipea ligulata*, Levinson, 1909, p. 140, pl. 2. figs. 8a-e.

Unilaminar, the frontal surface convex, with the marginal zoëcia facing partly outwards, the basal surface flat or concave. Branches composed of as many as nine rows of zoëcia, unjointed. Proximal cryptocyst less extensive than in *M. spicata*, usually prolonged into a thick calcareous spike or column (fig. 31), descending basally into the body-cavity, on one or both sides. When paired these spikes are not on the same level, one being usually just visible in frontal view, at the proximal end of the opesia, the other completely concealed by the cryptocyst and best seen in a basal view of a Canada balsam preparation. Spines 1, 1, well developed. Frontal avicularium single, symmetrical, its rostrum broadly triangular and directed proximally, shorter and wider than in *M. spicata*; not developed on the distal side of an ovicell. Internal avicularia (fig. 33) rather short, nearly horizontal, the base wide, the rostrum just appearing in the proximal end of the opesia. Ovicells longer than wide, the two calcareous bars uniting in a wide Gothic arch near the distal end, with a short median mucro. Basal walls of zoëcia strongly

constricted laterally, the arrangement being as in *Amastigia rudis* (Pl. 17. fig. 27), the basal wall correspondingly sinuate. Branches bordered by lateral groups of rootlets, as in the allied species, given off from pore-chambers at the proximal ends of the marginal zoecia. The terminal walls may or may not be provided with blister-like pore-chambers at their insertion into the basal wall.

Victorian specimens, Bracebridge Wilson Coll., in British Museum, 97.5.1.453,454.

Waters regards this as a unilaminar variety of *M. roborata*, but I think its characters entitle it to specific rank.

11. *MENIPEA ROBORATA* (Hincks). (Pl. 18. figs. 28-30.)

*Membranipora roborata*, Hincks, 1881, A. M. N. H. (5) viii. p. 128, pl. 2. figs. 3, 3a.

Curtis Id., Bass Straits; 1892, *Ibid.* (6) ix. p. 331.

*Flustra membraniporides*, Busk, 1884, p. 54, pl. 32. figs. 7 a, b. Port Jackson, Bass Straits.

*Craspedozoum roboratum*, MacGillivray, 1886, p. 131, pl. 1. fig. 4; 1889, Prodr. Zool. Vict., Dec. xviii. p. 284, pl. 177. figs. 4, 5, 5a. Victoria.

*Flabellaria roborata* (pars), Waters, 1898, J. L. S. xxvi. pp. 660, 662, 672.

*Flabellina* (*Flabellaria*) *roborata*, Levinsen, Vid. Medd. Naturh. Foren. Copenhagen, 1902, p. 21.

*Menipea roborata* (pars), Waters, 1897, A. M. N. H. (5) xx. p. 183.

*Menipea roborata*, Levinsen, 1909, pp. 3, 9, 131, 132, 139, pl. 2. figs. 7 a-k (*Flabellina* on plate).

Bilaminar, unjointed, pluriserial, with at least 17 rows of zoecia, the branches bordered by marginal bundles of rootlets, widening terminally and assuming an almost Flustrine appearance. Basal walls of the median zoecia only slightly constricted, laterally, near the middle. Spines 1, 1. Cryptocyst less developed than in *M. ligulata*. Thickening bars of ovicells uniting in the form of a Gothic arch and more or less acuminate; or in a rounded curve, without a mucro. Frontal avicularia paired (except on the lateral zoecia, where the avicularium is single) close together, the rostrum directed obliquely proximally; two constantly present on the distal side of an ovicell, widely separated, their direction reversed. Internal frontal avicularia large, directed nearly horizontally, on the basal side of the cryptocyst: their distal end visible at the proximal end of the opesia. Rootlet pore-chambers of the marginal zoecia inconspicuous. Blister-like pore-chambers on the proximal side of the insertion of the terminal walls into the basal wall present or absent.

The synonymy shows that there has been much difference of opinion with regard to the generic position of the present species; but I agree with Waters and others that it must be placed in *Menipea*. Hincks (1892) and Waters have both expressed the opinion that *M. ligulata* and *M. spicata* are varieties of this species. That it actually belongs to *Menipea* is indicated by *M. spicata*, which has the typical unilaminar character of the genus, while

retaining the characteristic position of the joint at the bifurcation. This species has a close resemblance to *M. spicata* in all essential details of structure; and its internal avicularia (figs. 29, 30) found also in other species (see Sect. III.) are a striking point of agreement. Another resemblance is the occurrence in both species of calcareous spines projecting into the body-cavity, as originally described by Levinsen. On separating the two laminae of a branch of *M. roborata*, after boiling in Eau de Javelle, it is found that while rosette-plates are wanting in all the zoecia of the median rows, typical lateral rosette-plates occur on all those of the two marginal rows. *M. ligulata* shows a distinct tendency to curve the margins of its branches towards the basal surface. If this process were continued until the edges united to form a hollow unilaminar cylinder, with the basal surface internal and the frontal surface external, and if this cylinder were then compressed so that the cavity disappeared and the basal walls of opposite sides came into contact, a bilaminar branch would result. At each lateral margin the external zoecia would be united by rosette-plates, while none of the others would be thus united. This is the arrangement actually found in *M. roborata*.

Specimens (slides) in the British Museum: 97.5.1.455, 457, Victoria, Bracebridge Wilson Collection; 81.10.21.352-354, Port Jackson; 50.5.2.2.

12. *MENIPEA VECTIFERA* \*, n. sp. (Pl. 17. fig. 23; Pl. 18. figs. 36-39.)

Unilaminar, the frontal surface flat, the basal surface also flat or slightly convex; the branches composed of as many as seven series of zoecia, and bordered by lateral bundles of rootlets. Apparently not normally jointed, although secondary breaks are formed across the branches, becoming converted into joints by the development of irregular chitinous tubes. Habit as in *M. spicata*, but less calcified. Cryptocyst (fig. 23) finely tubercular, the proximal part extensive, especially in the marginal zoecia, the free edge narrow on the distal side of an ovicell. A pair of long bars, expanding at their free ends in a palmate manner (figs 37, 39), descend from the thickened edge of the proximal cryptocyst into the body-cavity, their direction being nearly vertical, but with a slight slope proximally. Spines small, 2, 2, the inner or distal pair commonly vestigial and recognizable by their tubular cavities traversing the oral frame, as seen in a Canada balsam preparation. Frontal avicularium single, asymmetrical, commencing at one edge of the proximal cryptocyst, the rostrum directed transversely or slightly proximally, the mandible rather elongated and linear distally. On the distal side of an ovicell two frontal avicularia occur, widely separated, their rostra reversed so as to point distally and outwards. Internal avicularia (fig. 36) found in several cases in the more proximal zoecium of the two formed when a row is doubled, close to the concave side of the

\* *Vectis*, a bar; referring to the two bars borne by the proximal cryptocyst.

zoecium and directed more or less basally; concealed beneath the proximal cryptocyst in frontal view. Marginal avicularia (fig. 23), on the marginal zoecia, small, with a deep cavity excavated in the distal part of the outer calcareous wall. Basal surface of zoecia moderately constricted laterally, the terminal wall showing one, two, or even three blister-like pore-chambers projecting into the proximal zoecium, close to the basal wall. A conspicuous pore-chamber giving off a rootlet at the proximal end of each marginal zoecium, situated just distally to the marginal avicularium. A single basal heterozoecium (fig. 38) sometimes present at the angle of the bifurcation, its rostrum narrow and elongated distally. Ovicells without distinct thickening bars, the free edge of the ectozoecium forming a rounded curve, passing near the sides and distal margin, and not giving rise to a muero. Operculum distinct and Membraniporiform, without basal sclerite, but with well-marked lateral, triangular, ocluser flanges.

Described from three specimens in the British Museum Collection, all from New Zealand:—Hincks Collection, 99.5.1.630 (Type) and 458 (labelled *Membranipora roborata*); Busk Collection, 99.7.1.703 (labelled *Menipea multiseriata*).

This interesting species would be referable to *Craspedozoom* if that genus were recognized as distinct. In the presence of internal avicularia it agrees with the other three species which were placed in that genus by MacGillivray. But this feature allies the *Craspedozoom* group with typical species of *Menipea* such as *M. triseriata* and *M. marionensis*, while *C. spicatum* shows a further agreement with *Menipea* in the character of its jointing. The present species, in retaining a single basal heterozoecium at the bifurcation, indicates that these structures form a part of the original inheritance of the genus, as in other genera of Serupocellariidae, and notably *Amastigia* and *Notoplites*. The presence of marginal avicularia, which I have not found in other species of *Craspedozoom*, is a further feature of interest.

### 13. *MENIPEA MULTISERIATA*, Busk.

*Menipea multiseriata*, Busk, 1852<sup>2</sup>, p. 22, pl. 60, figs. 1, 2. New Zealand.

Unilaminar, multiserial, jointed, bordered by marginal groups of rootlets, the number of series of zoecia at least 8. Basal walls of the zoecia hardly contracted laterally. Spines 1, 1. Ovicells closely resembling those of *M. roborata*. Frontal avicularia 2 on the median zoecia, the rostrum directed obliquely proximally; two constantly present on the distal side of an ovicell, the rostrum directed nearly transversely outwards; one on the marginal zoecia. A small lateral avicularium on the marginal zoecia.

Busk considered this species nearly allied to *M. triseriata*, and possibly a variety of it. The locality was said to be unknown by him. The type-slide (99.7.1.112.D) was not returned to the Museum on the completion of the Catalogue, but it came later, with the remainder of the Busk Collection

received in 1899. It was then unnamed, but it had been marked by Busk "New Zealand." The specimen was determined by Mr Kirkpatrick, in 1904, as the missing type-slide. The evidence in favour of this view seems to me conclusive. A portion of the specimen exactly resembles Busk's fig. 1; and there are certain agreements between the specimen and the figure, particularly the occurrence of a minute emargination in the outer outline of the uppermost marginal zoecium, on the left side, which show that the figure had been drawn with great accuracy. It must therefore be assumed that Busk had obtained evidence; after the publication of his description, that the figured specimen came from New Zealand. It may here be noted that Waters (1887, A. M. N. H. (5) xx. pp. 84, 183), who does not admit the specific distinctness of *M. roborata* and the allied forms, and has stated that a New Zealand unilaminate form is jointed, may have had *M. multiseriata* under observation. It is possible, on the other hand, that he was referring to *M. rectifera*.

It is remarkable that the resemblance of *M. multiseriata* to *M. roborata* has not previously been noticed. I have felt some hesitation in separating them, but I think this procedure may be justified on the following grounds:—*M. multiseriata* is unilaminar. I do not think it is a specimen of *M. roborata* in which the laminae had become separated, because the marginal zoecia show no rosette-plates and because occasional rootlets pass across the basal surface. The species under consideration has marginal avicularia, which do not occur in *M. roborata*; and it is jointed, another definite difference. In a normal bifurcation of the type-specimen it appears to me that only one of the branches of the fork is jointed, and that in this one the joint traverses the opesia of the innermost zoecium. The jointed branch consists of only 2 or 3 zoecia at its base. In other parts, secondary joints occur as in certain other species of *Menipea*. The joint in these cases traverses the whole width of a branch, without having any relation to a bifurcation. It has clearly been formed by absorption of the calcareous matter, but the separate edges are joined by irregular chitinous tubes, which have the appearance of being new formations, and not simply the chitinous lining of the zone of the zoecium which lies in the region of the joint.

I have been unwilling to interfere with the type-specimen to the extent that would be necessary in order to obtain evidence with regard to the occurrence of internal avicularia; and I must leave this point undecided.

### 3. NOTOPLITES\*, n. gen. Genotype, *N. rostratus*, n. sp.

*Cellularia* (pars)<sup>†</sup>, *Menipea* (pars), and *Scrupocellaria* (pars), auctt.

Bifurcation of type 15 (fig. 15), one or both branches jointed, the proximal segments of F and G in contact and much longer than the corresponding

\* *νῶτον*, back; *ἐπλίρης*, an armed man; in allusion to the basal avicularia.

parts of J and K. The joints are on the distal side of C and D, and traverse the proximal ends of GK and FJ without passing through an opesia. Rootlets given off on the distal side of the joint. Zoecia elongated, the opesia relatively short. Basal avicularia, approaching a vibraculoid form, typically present, and then usually confined to the neighbourhood of the axils; the rootlets given off by them or from other parts closely applied to the margins of the branches and strengthening the axils. Scutum, frontal and marginal avicularia present or absent. Ovicells typically large, and with a frontal fenestra. Zoarium biserial.

I propose this genus primarily for several deep-water species represented in the 'Siboga' Collection, all of them supported by an elongated stalk composed of parallel rootlets, which diverge at the base to form an anchoring tuft—a type of growth frequently found in Cheilostomes from deep water. I select as the genotype *N. rostratus*, of which I give a preliminary diagnosis; this species representing the genus in what I consider the full expression of its characters, some of which are lost in other species. The features which I regard as specially characteristic are: (1) the mode of bifurcation, the joints being at a considerable distance from the axil (a convenient way of recognizing members of the genus), and the position of the joints, which are completely on the distal side of C and D; (2) the occurrence of basal heterozoecia, commonly confined to the bifurcations. Certain species do not possess these structures, but their affinity is indicated by the mode of branching.

*Notoplites* appears to be allied to *Amastigia*, as shown by the occurrence of basal avicularia; but it differs from that genus in being biserial and jointed, in the longer zoecia, and in having the basal avicularia confined, as a rule, to the bifurcations. It differs from *Menipea* in the fact that the joint does not traverse the opesia of the inner zoecium at a bifurcation. It will be observed that the genus, as here understood, occurs from the Arctic to the Antarctic Oceans, but that a connecting-link is afforded by the 'Siboga' species, from the neighbourhood of the equator.

#### 1. *NOTOPLITES ROSTRATUS*, n. sp.

Zoarium reaching a length of 55 mm., attached by a proximal tuft of rootlets which separate from a main stem, about 20 mm. long, composed of parallel rootlets. Zoecia long and narrow, their outer outline concave; the opesia, which occupies less than half the frontal length, oval, much reduced proximally by a broad, crescentic cryptocyst. Distal spines 2 external, 1 median, 1 internal, with another arising from the basal surface. Scutum jointed at the base, the lamina lobed, its distal portion the smaller and generally acutely pointed and narrow. Frontal avicularium, in ordinary zoecia, variable in size, elevated, at some distance from the opesia, on the inner side of the cryptocyst, reclining against the opesia of the preceding



alternate zoecium, the rostrum linear and directed obliquely inwards and distally. Frontal avicularium succeeding an ovicell gigantic, directed transversely outwards, the upcurved rostrum resting on the distal border of the ovicell, the much elongated linear mandible on the distal side. Marginal avicularia varying in size, usually small, the rostrum directed obliquely outwards, basally and proximally; occasionally gigantic; on the fertile zoecia gigantic, originating slightly on the basal side, the rostrum directed distally, nearly parallel to the edge of the branch, the distal half free, the mandible on the outer side. Basal avicularia (one pair) occur on the inner zoecia succeeding the joints, inflated proximally, the long linear rostrum directed distally; each giving off a rootlet at its proximal end, in line with itself, the rootlet running closely attached to the margin of the axil. Ovicells large and very long, imperforate except for a transversely elongated fenestra, on the frontal surface, near the orifice.

'Siboga' Expedition, Stat. 211, 5° 40' 7" S., 120° 45' 5" E., 1158 metres.

Various species which have been referred to other genera appear to belong to *Notoplites*; and, in some of these, basal avicularia have already been described or have been found by me in specimens in the British Museum Collection. In other species basal avicularia seem to be wanting; but here, as in other genera of *Scrupocellariidæ*, it may be assumed that an important generic character may fail to develop, the affinities of the species being indicated mainly by the mode of bifurcation.

(a) *Species in which basal avicularia occur.*

2. *NOTOPLITES BILOBA* (Busk).

*Cellularia biloba*, Busk, 1884, p. 18, pl. 3. figs. 2-2 b. Azores, 900 fathoms.

Resembling *N. rostratus* in habit, in the form of its zoecia, scutum, marginal avicularia, and ovicells. Frontal avicularia wanting. The 'Challenger' slides (87.12.9.63, 64) show a pair of small transverse basal avicularia, which were not noticed by Busk, at the bifurcation.

3. *NOTOPLITES CRATERIFORMIS* (Busk).

*Cellularia crateriformis* Busk, 1884, p. 16, pl. 3. figs. 1-1 b. E. of Buenos Aires, 1900-2650 fathoms.

Resembling the preceding species in habit and in the marginal avicularia. Scutum and frontal avicularia wanting. Of the 'Challenger' slides (87.12.9.51, 52) 51 shows a pair of small basal avicularia, directed nearly transversely, at a bifurcation. These seem to be referred to by Busk, who says: "Occasionally a radical tube may be seen supporting, instead of an ordinary zoecium, a small curiously formed avicularium."

4. NOTOPLITES AVICULARIÆ (*Yanagi & Okada*).

*Scrupocelluria aviculariæ*, Yanagi & Okada, 1918, Ann. Zool. Japon. ix. p. 413, pl. vi. fig. 4, text-fig. 4. Japan, 78 fathoms.

Scutum large, with a complicated cavity. Frontal and marginal avicularia small. Basal avicularia small, the rostrum directed obliquely proximally and inwards, not confined to the bifurcations, but occurring alternately, on the proximal ends of the zoœcia. The text-figure shows clearly the origin of a rootlet from a basal avicularium.

5. NOTOPLITES MARSUPIATUS (*Jullien*).

*Scrupocelluria marsupiatæ*, Jullien, 1882, Bull. Soc. Zool. France, vii. p. 506, pl. 13. figs. 17-20. N.W. of Spain, 2018 metres; 1888, Mias. Sci. Cap Horn, vi. Zool. p. 69.

" " Calvet, 1907, Exp. Sci. 'Travailleur' et 'Talisman,' viii. p. 377.

" " Waters, 1888, 'Challenger' Rep. pt. lxxix. p. 9.

*Menipea clausa*, Busk, 1884, p. 20, pl. iv. figs. 5, 5a. W. of Azores, 1675 fathoms.

Jullien and Waters both pointed out in the same year (1888) that Busk's species is a synonym of *S. marsupiatæ*. A special peculiarity of the species is that the convex scutum so completely fills the opesia that it appears at first sight to be the frontal wall. It is attached to its stalk at the distal inner corner, and its free border is marked by characteristic radial slits, in the 'Challenger' specimen (87.12.9.83) at least. Frontal and marginal avicularia small. Jullien states that he found a single basal vibraculum in this species, and Waters points out that Kirkpatrick has found vibracula on the basal side, on two zoœcia.

(b) *Species in which basal avicularia are not recorded.*

6. NOTOPLITES ELONGATUS (*Busk*).

*Cellularia elongata*, Busk, 1884, p. 19, pl. 3. figs. 3-3b. Kerguelen, 28 fathoms.

Scutum elongated, the distal lobe the smaller. The 'Challenger' slides (87.12.9.65, 66) show that this species agrees in its bifurcation with *Notoplites*. Marginal avicularia small, frontal avicularia wanting. I cannot find any case in which two median zoœcia occur, as shown in Busk's fig. 3a.

7. NOTOPLITES JEFFREYSII (*Norman*).

*Menipea jeffreysii*, Norman, 1868, Q. J. M. S. (n. s.) viii. p. 213, pl. 5. figs. 4-8\*. Shetland; 1893, A. M. N. II. (6) xii. p. 446, pl. 19. fig. 1. Hardanger and Trondhjem Fjorde, Finmark; 1903, *Ibid.* (7) xi. p. 579.

" " Hincks, 1880, p. 42, pl. 9. figs. 1, 2. Shetland.

" " Nordgaard, 1918, Tromsø Mus. Aarsheft. xl. (1917), p. 35.

In his 1893 paper Norman pointed out that the scutum is not correctly described in his original account and in Hincks' fig. 1, also referring to the

\* The figures are wrongly given in the text as 3-5, as pointed out by Norman (1903. p. 446).

original specimen, but that it fills the entire opesia (in the same way as in *N. marsupiatius*, Jull.). He refers to a figure by Alder, reproduced in his own original account (fig. 6), supposing that certain avicularia which appear to be on the basal surface are really frontal avicularia seen through the zoecia by transparency. It appears possible that these are really basal avicularia, and in a specimen from Norway in the Cambridge Collection I have observed structures on the basal surface which may perhaps be of this nature.

#### 8. NOTOPLITES SMITTH (*Norman*).

*Cellularia ternata*, forma *duplex*, Smitt, 1868, Öfv. K. Vet.-Akad. Förh. xxiv. (1867), pp. 283, 312, pl. 16. figs. 25, 26. Spitsbergen.

*Menipea smittii*, Norman, 1868, Q. J. M. S. (n. s.) viii. p. 214.

" " Hincks, 1880, p. 43.

*Menipea duplex*, Levisen, 1887, *Dijmphna-Togtets zool.-bot. Udbytte* (Copenhagen), p. 309, pl. 26. figs. 1, 2. Kara Sea.

*Scrupocellaria smittii*, Waters, 1900, J. L. S. xxviii. p. 57, pl. 7. figs. 8-11. Franz Josef Land.

Hincks remarks of this species, which has frontal and lateral avicularia but no scutum, that it is nearly allied to *M. jeffreysii*. The mode of branching characteristic of the genus may be seen in Smitt's fig. 25; but it is better shown by Waters (fig. 8), who emphasizes its difference from certain other species.

#### 9. NOTOPLITES ANTARCTICUS (*Waters*).

*Scrupocellaria antarctica*, Waters, 1904, 'Belgica' Bryozoa, p. 25, pl. 1. figs. 5 a-e; pl. viii. figs. 2 a, b. Antarctic, 435-480 metres.

" " Kluge, 1914, p. 606, pl. 28. fig. 1. Antarctic, 350-385 metres.

Frontal and marginal avicularia and scutum present. Waters' fig. 5 a shows the mode of bifurcation well.

The three species next following, described by Kluge from Antarctic waters, may be referred to *Notoplites*, on the evidence of the bifurcation, as shown in the figures. *S. watersi* appears to bifurcate in the same manner; while *S. perdita*, in which there is no evidence with regard to this point, has an ovicell resembling that of other species of *Notoplites*.

#### 10. NOTOPLITES TENUIS (*Kluge*).

*Scrupocellaria tenuis*, Kluge, 1914, p. 608, pl. 27. fig. 2. Antarctic, 46-385 metres.

Frontal avicularia and scutum present. Marginal avicularia wanting. Bifurcation clearly represented.

#### 11. NOTOPLITES DRYGALSKII (*Kluge*).

*Scrupocellaria drygalskii*, Kluge, 1914, p. 609, pl. 27. fig. 5. Antarctic, 70-385 metres.

Frontal and marginal avicularia present. The scutum fills the opesia, as in *N. jeffreysii*. Bifurcation figured.

12. NOTOPLITES VANHÖFFENI (*Kluge*).

*Scrupocellaria vanhoeffeni*, Kluge, 1914, p. 610, pl. 27. fig. 6. Antarctic, 350-385 metres.

Frontal and marginal avicularia and scutum present; differing from the preceding species in the scutum, which has a complicated or "cervicorn" cavity. Bifurcation figured.

13. NOTOPLITES WATERSI (*Kluge*).

*Scrupocellaria watersi*, Kluge, 1914, p. 607, pl. 27. fig. 2. Antarctic, 350-385 metres.

Frontal and marginal avicularia and scutum present. The bifurcation represented in the figure is typical except for the zoæcium B. I suspect that a mistake was made with regard to this point.

14. ? NOTOPLITES PERDITUS (*Kluge*).

*Scrupocellaria perdita*, Kluge, p. 613, text-fig. 2. Antarctic, 2450 metres.

Bifurcation not described. The scutum and ovicell resemble the corresponding parts in *N. rostratus*.

*Incertæ sedis* (possibly belonging to *Notoplites*).

15. MENIPEA NORMANI, *Nordgaard*, 1900, *Norske Nordhavs-Exp.*, p. 4, pl. i. figs. 2-8. Off Norway, 408-1134 metres.16. ? NOTOPLITES SIMPLEX (*Kluge*).

*Scrupocellaria simplex*, Kluge, 1914, p. 607, pl. 27. fig. 1. Antarctic, 385 metres.

Branches biserial, the opesia elongated, oval, with much raised margin. Scutum and spines wanting. A single frontal avicularium, and occasionally a minute marginal avicularium. Ovicells unknown, basal heterozoecia not described. Rootlets at first passing down the margins of the branches, given off from a chamber at the proximal end of the zoæcium. Kluge states that this species is ordinarily unjointed, but that the branches may be jointed "oberhalb der Gabelung." The zoæcium and the opesia resemble the corresponding parts of *Notoplites elongatus* (Busk); and it seems possible that the species should be referred to the same genus.

4. TRICELLARIA, *Fleming*.

*Tricellaria*, Fleming, 1828, p. 540.

*Cellarina*, Van Benedeu (*para*), 1848, p. 70 (nec *Cellarina*, D'Orbigny, 1851, p. 181).

*Ternicellaria*, D'Orbigny, 1851, pp. 40, 47.

*Bugulopsis*, Verrill, 1880, p. 190.

*Cellularia* (*para*) and *Menipea* (*para*), auctt.

Zoarium jointed, the branches biserial. Internodes commonly constituted by three zoæcia, at least in the main stems. Zoæcia more elongated than in *Emma*, the opesia occupying a small proportion of the front and without a

large development of cryptocyst proximally. Bifurcation of types 9-12 (figs. 9-12), the joints traversing the proximal ends of the zoecia CG and DF; one or other of the joints occasionally suppressed. F and G usually separated on the basal side of E, sometimes by its whole width, their proximal segments shorter than the corresponding parts of C and D. The proximal ends of F and G may be suppressed, in which case the internode consists of a single zoecium at its proximal end, and the joint consists of a single chitinous tube. Rootlet given off on the proximal side of the joint. Scutum, marginal and frontal avicularia present or wanting. Basal avicularia and vibracula wanting, but probably represented by the rootlet pore-chamber.

Among the species which I include in *Tricellaria* are the following:—

A. Internodes biserial at the proximal end. Joints composed of two chitinous tubes (figs. 9-11).

1. *TRICELLARIA TERNATA* (Ell. & Sol.). (Fig. 9.)

*Cellaria ternata*, Ellis & Solander, 1786, p. 30. Aberdeen.

*Menipea ternata*, Hincks, 1880, p. 38, pl. 6. figs. 1-4. British coasts.

This common species has often been described. I may draw attention to the possibility, mentioned on p. 324, that the structure from which a rootlet may arise in this species may represent a basal heterozoecium—a structure otherwise absent in the genus.

1 a. *TRICELLARIA TERNATA* (Ell. & Sol.), var. *GRACILIS*, Smitt.

*Cellularia ternata*, forma *gracilis*, Smitt, 1808, Öfr. K. Vet.-Akad. Förh. xxiv. (1867), pp. 282, 305, pl. 16. figs. 10-16. Spitzbergen to Britain and Belgium.

*Menipea gracilis*, Busk, 1878, in Nares, Narr. Voy. Polar Sea 'Alert' and 'Discovery,' ed. by H. W. Feilden, ii. p. 284.

It may be observed that *gracilis* as the trivial name of this form is antedated by *Cellarina gracilis*, Van Beneden, 1848 (see Sect. II.).

2. *TRICELLARIA OCCIDENTALIS* (Trask), 1873 \*. (Fig. 10.)

*Menipea occidentalis*, Trask, 1873, Proc. Calif. Acad. Nat. Sci. i. (1854-1857), 2 ed. p. 113, pl. 4. fig. 4.

" " Robertson, 1905, Univ. Calif. Publ., Zool. ii. p. 254, pl. 6. figs. 22-25. California.

" *compacta*, Hincks, 1882, A. M. N. H. (5) x. p. 461. Queen Charlotte Is.

3. *TRICELLARIA PRIBILOFI* (Robertson).

*Menipea pribilofi*, Robertson, 1905, *l. cit.* p. 257, pl. 7. figs. 32, 33; pl. 8. fig. 34. Alaska, islands of Bering Sea.

\* The Proceedings of the California Academy for 1854-1857 were originally printed in a newspaper, "The Pacific," but were republished, *verbatim*, in 1873. Dr. Trask's paper was read at the meeting, Mar. 30, 1857.

4. TRICELLARIA SYMPODIA (*Yanagi & Okada*).

*Menipea sympodia*, Yanagi & Okada, 1918, Ann. Zool. Japon. ix. p. 410, pl. 6. fig. 1, text-fig. 2. Japan, 250 fathoms.

As indicated by its name, this species is an instance of the sympodial mode of growth, due to the suppression of one of the joints at the bifurcation. The remarkably elongated, cylindrical frontal avicularia resemble those of *Menipea crispa* and of ? *Notoplites normani*.

5. TRICELLARIA PEACHII (*Busk*). (Fig. 11.)

*Cellularia peachii*, Busk, 1851, A. M. N. II. (2) vii. p. 82, pl. 8. figs. 1-4. British coasts; Busk, 1852<sup>2</sup>, p. 20, pl. 27. figs. 3-5.

This common species has been frequently described. It appears to represent the extreme amount of loss of structures which typically occur in the genus, as shown by the disappearance of the frontal and marginal avicularia and of the scutum. It was made the genotype of *Bugulopsis* by Verrill; but its mode of bifurcation is that of *Tricellaria*, with which I think it should be placed.

6. TRICELLARIA MONOTRYPA (*Busk*).

*Cellularia monotrypa*, Busk, 1852<sup>1</sup>, p. 308. Bass Straits.

„ *cuspidata*, Busk, 1852<sup>2</sup>, p. 19, pl. 27. figs. 1, 2; 1884, p. 17.

In 1884 Busk remarked that it might be proper, conditionally, to revert to his original name, *monotrypa*. There seems no question that this should be done, as Busk was not justified by the Rules of Nomenclature in substituting a new name without adequate reason, which was not given in his second work published in 1852.

B. Internodes uniserial at the proximal end. Joints composed of a single chitinous tube (fig. 12).

I regard this condition as secondary, and as due to the suppression of the proximal segments of the zoecia F and G. A similar suppression is found in *Emma*.

7. TRICELLARIA ACULEATA (*D'Orb.*). (Fig. 12.)

*Bicellaria aculeata*, D'Orbigny, 1839-1846, Voy. Amér. Mérid. v. 4, p. 8, pl. 2. figs. 1-4 (*Tricellaria aculeata* on the plate). Falkland Is.

*Menipea aculeata*, Busk, 1884, p. 20, pl. 4. figs. 2, 2a. Falkland Is., Patagonia, 5-175 fathoms\*.

„ „ Marcus, 1921, Vid. Medd. Dansk naturh. Foren. lxxiii. p. 93. Campbell Id.

\* Busk's record of Stat. 303, 1325 fathoms, should probably have been Stat. 308, 175 fathoms (see under *Amastigia benemunita*, p. 334).

- Menipea fuegensis*, Busk, 1852<sup>2</sup>, p. 21, pl. 19. figs. 1-3. Tierra del Fuego, Falkland Is.; 1879, Phil. Trans. vol. 168, p. 194. Kerguelen.  
 " " Jullien, 1888, Miss. Sci. Cap Horn, vi. p. 70, pl. 12. figs. 1, 2; pl. vii. figs. 8-10. Tierra del Fuego.  
*Scrupocellaria fuegensis*, Waters, 1904, 'Belgica' Bryozoa, p. 24. Straits of Magellan.  
 " *bifurcata*, Kluge, 1914, p. 614, text-fig. 3. Kerguelen.

There is some uncertainty with regard to *T. aculeata* and its synonyms. In 1879 Busk expressed the opinion that *Menipea fuegensis* (Busk, 1852) is a synonym of *M. aculeata*; and I think this opinion is correct. The type-specimen (54.11.15.262) of *M. fuegensis* is from the Falkland Islands, and it is of rather coarser habit than those described and figured in the 'Challenger' Report; while its scutum is linear instead of being branched. The scutum is known to be variable, within the limits of a single species, or even of the same colony, in other Scrupocellariidæ; and the differences in question do not seem to be sufficient for the establishment of two species from material from substantially the same locality. The fertile internodes figured by Jullien as *M. fuegensis* and by Kluge as *Scrupocellaria bifurcata* are very long, and Waters has expressed the opinion that Jullien's species should be considered distinct. I am inclined to regard them as different forms of a single species, as indicated in my synonymy. D'Orbigny's figures are probably not correct in all details, but some latitude must be allowed to observations made so long ago. All the specimens I have examined in the British Museum Collection, whether from the Falkland Islands, Patagonia, or Kerguelen, agree in the important character of having the internode composed of a single zoecium at its proximal end, associated with the existence of a single chitinous tube, instead of two tubes, in each joint.

#### 8. TRICELLARIA LONGISPINOSA (*Yanagi & Okada*).

*Menipea longispinosa*, Yanagi & Okada, 1918, Ann. Zool. Jap. ix. p. 408, pl. 6. fig. 3, text-fig. 1. Japan, 312 fathoms and depth not stated.

#### 5. EMMA, *Gray*.

*Emma*, Gray, 1843, p. 293.

" Busk, 1852<sup>2</sup>, p. 27.

*Menipea (pars)*, auctt.

Internodes very short, typically composed of two or three zoecia. Bifurcation of types 13, 14 (figs. 13, 14), the two branches given off symmetrically or asymmetrically. Opesia reduced by an extensive development of cryptocyst, sloping considerably in a basal direction. Marginal avicularia on the proximal side of the opesia, or opposite its proximal end. Scutum usually present, sometimes wanting. Joints conspicuous, the internodes very narrow proximally.

Gray gave no generic characters, which were later described by Busk. Although the genus has been considered unnecessary by MacGillivray (1881,

Prodr. Zool. Vict., Dec. vi. p. 32) and others, I think it may conveniently be retained for the following group of southern species. As pointed out by Busk, *Emma* is nearly related to *Tricellaria*.

A. Internodes biserial at the proximal end. Joints composed of two chitinous tubes (fig. 14).

1. *EMMA CRYSTALLINA*, Gray.

*Emma crystallina*, Gray, 1843, p. 293. New Zealand.

" " Busk, 1852<sup>2</sup>, pp. 28, 33, pl. 40. figs. 1-3. New Zealand, Bass Straits.

*Menipea crystallina*, MacGillivray, 1881, Prodr. Zool. Vict., Dec. vi. p. 31, pl. 58. figs. 2-2*b*.

" " Waters, 1887, A. M. N. H. (5) xx. pp. 88, 205. New South Wales, etc.

" " Levinsen, 1909, pp. 132, 133, pl. 2. figs. 1*a*, 1*b*.

2. *EMMA TRICELLATA*, Busk.

*Emma tricellata*, Busk, 1852<sup>2</sup>, pp. 28, 33, pl. 41. figs. 1, 2. Bass Straits, New Zealand.

*Menipea tricellata*, MacGillivray, 1881, *t. cit.* p. 34, pl. 58. figs. 5-5*b*.

3. *EMMA BUSKII* (Wyr. Thoms.) (fig. 14).

*Menipea buskii*, Wyville Thomson, 1858, Nat. Hist. Rev. v. Proc. of Societies, p. 144, pl. 12. fig. 1. Tasmania, New Zealand.

" " MacGillivray, 1881, *t. cit.* pp. 35, 32, pl. 58. figs. 6-6*b*.

" *buskii*, Levinsen, 1909, pp. 59, 131-133, pl. 2. figs. 3*a*-3*c*.

4. *EMMA CERVICORNIS*, MacGill.

*Emma cervicornis*, MacGillivray, 1869, Trans. Proc. R. Soc. Vict. ix. p. 127. Victoria.

*Menipea cervicornis*, MacGillivray, 1881, *t. cit.* pp. 34, 32, pl. 58. figs. 4-4*b*.

" " var., Waters, 1887, A. M. N. H. (5) xx. p. 88, pl. 4. fig. 1. New South Wales.

" " Levinsen, 1909, pp. 59, 132, 133, pl. 2. figs. 4*a*, 4*b*.

B. Internodes uniserial at the proximal end. Joints composed of a single chitinous tube (fig. 13).

5. *EMMA CYATHUS* (Wyr. Thoms.) (fig. 13).

*Menipea cyathus*, Wyville Thomson, 1858, *t. cit.* p. 143, pl. 15. figs. 10, 10*a*. Bass Straits; Port Fairy (Victoria).

" " MacGillivray, 1881, *t. cit.* pp. 33, 32, pl. 58. figs. 3-3*b*.

" " Levinsen, 1909, pp. 132, 133, pl. 2. figs. 2*a*, 2*b*.

6. *SORUPOCELLARIA*, Van Beneden.

Zoarium jointed, biserial, bifurcation of type 8 (fig. 8), the joints crossing the zoecia OG and DF; frequently traversing the opesia of the outer zoecia, C and D, but never those of F and G. Proximal segments of F and G in contact on the basal side of E, shorter than the corresponding parts of



C and D. Rootlets not forming marginal bundles, some of them given off by basal heterozoeæia. Each zoecium is typically provided with frontal and marginal avicularia and with a basal vibraculum, the last at its proximal end, the marginal avicularium at its distal end. Cavity of the vibraculum divided by a calcareous septum into a larger chamber containing the muscles, and a smaller chamber, from which a rootlet originates in the proximal members of the colony at least. Seta of the vibraculum without lateral branches.

This genus is readily recognizable, and as but little confusion exists with regard to its limits, I do not think it necessary to discuss the species in detail. The relations of the joints to the outer zoæcia at the bifurcations give useful assistance in characterizing species; a point which will be brought out more fully in my forthcoming Siboga Report. In some cases, as in fig. 8, the joint traverses the opesia at its middle. In other cases it merely involves the proximal end of the opesia; and in others it passes entirely on the proximal side of that opening.

Kluge (1914) has described 17 species which he refers to *Scrupocellaria*. One of these, *S. bertholletii*, Aud. (p. 616) is from Cape Verde, and is rightly placed. The remainder are from Kerguelen (1 species) and Antarctic localities (15 species). All of these may more properly, in my opinion, be distributed among the genera *Amastigia*, *Notoplites*, *Menipea*, and *Tricellaria*, and I think it has still to be proved that the genus occurs within the limits of the Antarctic Circle. *Scrupocellaria* is a characteristic genus of Northern latitudes, it is well represented in the Siboga Collection from near the Equator, and it is well known to occur in localities much further south, as for instance off the south coast of Australia. Its possible relation to *Amastigia* is indicated on p. 337, under *A. kirkpatricki*.

Although *Scrupocellaria* exhibits the tendency, shown in other members of its Family, to suppress important structures like the scutum and the frontal and marginal avicularia, all these structures are more commonly retained than in certain other genera. The basal vibracula are very rarely wanting; and in most cases they occur regularly on every zoecium. The occurrence of either one or two vibracula in the axil of the bifurcation is a useful systematic character, as has been pointed out by Waters (1897, J. L. S. xxvi, p. 7). Levinsen (1909, p. 134) has stated that the vibraculum of *Scrupocellaria* is not divided into two chambers. I do not understand this assertion, which is at variance with my own results.

## EXPLANATION OF THE PLATES.

The drawings made with an A objective were reduced to  $\frac{1}{2}$ , and those with a C objective to  $\frac{1}{3}$  their original size.

## PLATE 16.

*Diagrams of bifurcation in Cellularine genera* (Text, Sect. IV.). The branches are all seen from the basal surface, and a uniform notation has been adopted for the zoecia, of which A is the more proximally situated zoecium which gives rise to two distal successors. The preparations from which the drawings were made were, in nearly all cases, Canada balsam mounts.

- Fig. 1.—Type 1. *Didymozoum triseriale* ('Siboga').  
 Fig. 2.—Type 2. *Stirpariella* (undescribed species in the 'Siboga' Collection).  
 Fig. 3.—Type 3. *Bugula johnstonei* ('Siboga'); c.p., connecting process.  
 Fig. 4.—Type 4. *Bugula scaphoides* ('Siboga'); „ „ „  
 Fig. 5.—Type 5. *Bugula dentata* ('Siboga'); „ „ „  
 Fig. 6.—Type 6. *Euplozoum cirratum* ('Siboga'). The dotted lines indicate the joints.  
 Fig. 7.—Type 7. *Kinetoskias* (undescribed, 'Siboga' Collection).  
 Fig. 8.—Type 8. *Scrupocellaria ferov* ('Siboga'). The joint traverses the opesia (dotted lines) of the outer zoecia.  
 Fig. 9.—Type 9. *Tricellaria ternata* (Norway). A rootlet occurs on the proximal segment of D.  
 Fig. 10.—Type 10. *Tricellaria occidentalis* var. *dilatata* (Japan); r., rootlet.  
 Fig. 11.—Type 11. *Tricellaria peachii* (Durham coast).  
 Fig. 12.—Type 12. *Tricellaria aculeata* ('Challenger,' Stat. "303," but probably Stat. 308; see text, p. 355).  
 Fig. 13.—Type 13. *Emma cyathus* (Bass Straits).  
 Fig. 14.—Type 14. *Emma buskii* (Victoria).  
 Fig. 15.—Type 15. *Notoplites rostratus*, n. sp. ('Siboga'). A rootlet occurs on the distal segment of K.

## PLATE 17.

Figs. 16–20. Diagrams of bifurcation, continued. The specimens from which figs. 21 and 23–27 were drawn had been cleaned with Eau de Javelle, involving the loss of the spines and chitinous parts.

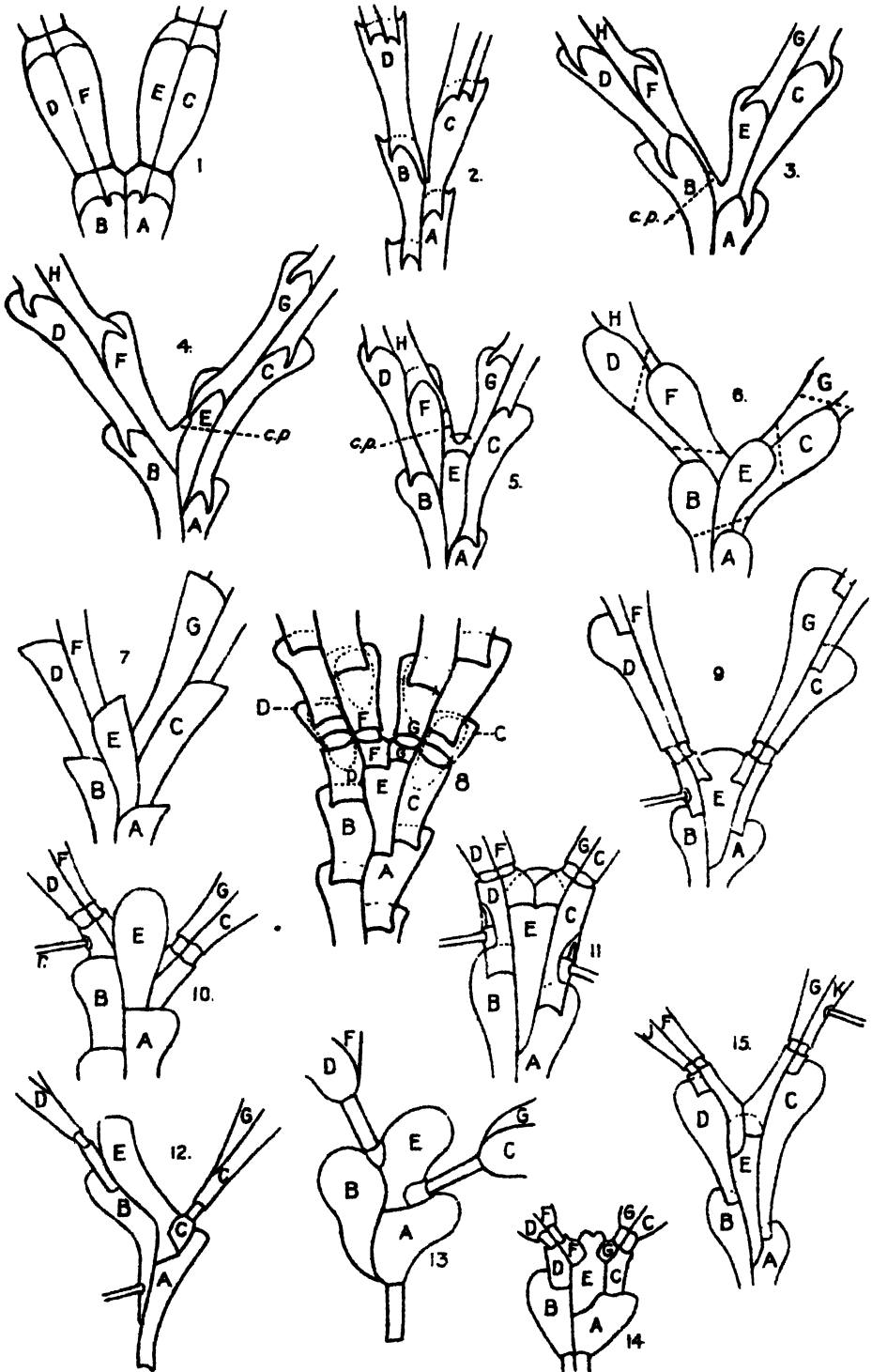
- Fig. 16.—Type 16. *Cornucoquina* (from a specimen in the 'Siboga' Collection); r.p., rosette-plates.  
 Fig. 17.—Type 17. *Menipea crispa* (Algoa Bay, S. Africa). The joint traverses the opesia (dotted lines) of the inner zoecia.  
 Fig. 18.—Type 18. *Menipea triseriata* (Simon's Bay, S. Africa, B.M. 87.12.9.90).  
 Fig. 19.—Type 19. *Menipea apicata* (Victoria). A system of branches, showing a sympodial form of colony, associated with the suppression of one of the joints at each bifurcation (B.M. 97.5.1.400).  
 Fig. 20.—Type 20. *Amastigia kirkpatricki* (Lev. MSS.), n. sp. (Marion Id., B.M. 87.12.9.97).  
 Fig. 21.—*Amastigia nuda* (Victoria, B.M. 97.5.1.240). Frontal view. Obj. A.

- Fig. 22.—*Menipea marionensis* (Simon's Bay, S. Africa, 'Challenger,' B.M. 87.12.9.99; found with *M. triseriata*). Basal view, showing 4 internal avicularia (*i.av.*); *l.av.*, lateral avicularium. Obj. A.
- Fig. 23.—*Menipea vectifera*, n. sp. (New Zealand, B.M. 99.5.1.630). Frontal view. Obj. A.
- Fig. 24.—*Amastigia nuda* (Tierra del Fuego, B.M. 54.11.15.87, type-specimen). Diagram of basal surface; *l.av.*, lateral avicularium; 1, 5, marginal zoecia; 3, median zoecium; 2, 4, submedian zoecia.
- Fig. 25.—*Amastigia nuda* (Victoria, B.M. 97.5.1.246). Basal view of a 5-serial branch, showing 4 basal avicularia and 2 ovicells on marginal zoecia. Obj. A.
- Fig. 26.—*Amastigia rudis* (Victoria, B.M. 97.5.1.462). Frontal view, showing gigantic frontal avicularia on the marginal zoecia. Obj. A.
- Fig. 27.—*Amastigia rudis*. Basal view of the same branch, a seta having been inserted from another specimen which was not cleaned with Eau de Javelle. Obj. A.

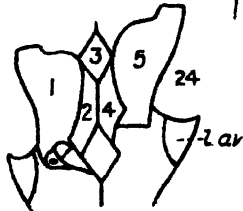
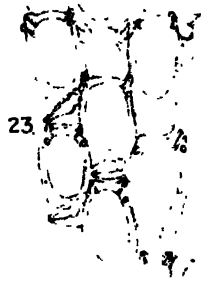
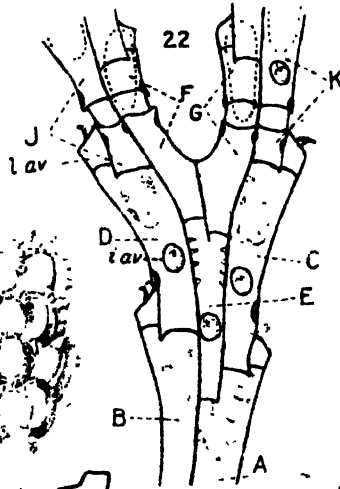
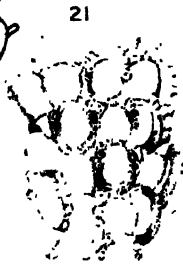
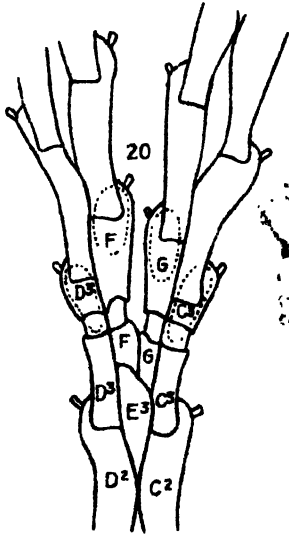
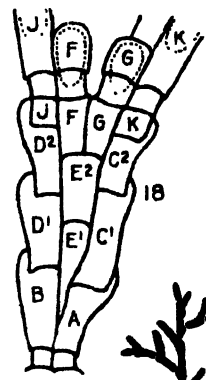
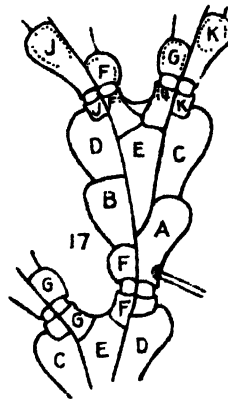
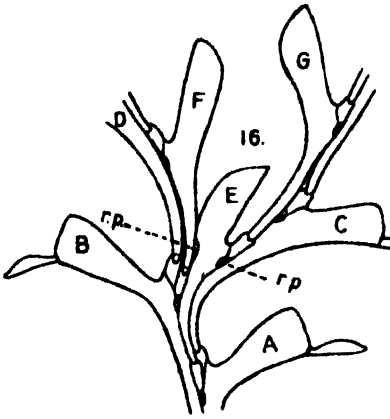
## PLATE 18.

All the drawings are from specimens which had been boiled with Eau de Javelle, after which treatment the longitudinal rows can be separated by gentle pressure of a needle on the basal surface. The drawings were made with a C objective and reduced to one-third their original size.

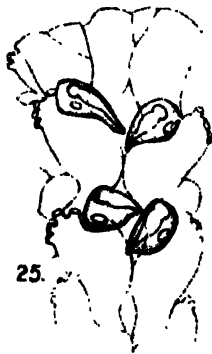
- Fig. 28.—*Menipea roborata* (Australia, B.M. 50.5.2.2). Lateral view of two zoecia, with ovicells (*ov.*) and frontal avicularia (*f.av.*); *l.r.p.*, lateral rosette-plates; *sp.*, base of spine; *i.sp.*, internal calcareous spines.
- Fig. 29.—*Menipea roborata* (same slide). Lateral view of two zoecia without ovicells; *f.av.*, frontal avicularium; *i.av.*, internal avicularium; *t.r.p.*, terminal rosette-plate.
- Fig. 30.—*Menipea roborata* (same slide). Frontal view; *cr.*, the part of the cryptocyst which overlies the internal avicularium (*i.av.*), of which the proximal end (*p.*) is seen partly through the frontal wall and partly through the lateral wall of the zoecium; *t.r.p.*, terminal rosette-plate.
- Fig. 31.—*Menipea ligulata* (Victoria, B.M. 97.5.1.454). Lateral view, showing two ovicells, a frontal avicularium, and a strong calcareous process (*c.p.*) projecting vertically into the body-cavity at the proximal end of the opesia.
- Fig. 32.—*Menipea spicata* (Victoria, B.M. 83.10.15.46). Lateral view of two zoecia without ovicells; *f.av.*, frontal avicularium; *i.av.*, internal avicularium.
- Fig. 33.—*Menipea ligulata* (Victoria, B.M. 97.5.1.454). Frontal view of a zoecium with an ovicell and an internal avicularium (*i.av.*).
- Fig. 34.—*Menipea spicata* (same slide as fig. 32).—Lateral view of two zoecia, each with an ovicell produced into a conspicuous spike.
- Fig. 35.—*Menipea spicata* (same slide). Basal view; two of the zoecia with internal avicularia (*i.av.*); *r.*, origin of marginal rootlet.
- Fig. 36.—*Menipea vectifera*, n. sp. (New Zealand, B.M. 99.5.1.630). Basal view of two zoecia, one with an internal avicularium (*i.av.*).
- Fig. 37.—*Menipea vectifera*, n. sp. (same slide). Basal view of two zoecia, showing the characteristic calcareous bars (*c.b.*) projecting into the body-cavity from the proximal cryptocyst.
- Fig. 38.—*Menipea vectifera*, n. sp. (same slide). Basal view, showing the large basal avicularium (*b.av.*) at the bifurcation; *l.av.*, lateral avicularium.
- Fig. 39.—*Menipea vectifera*, n. sp. (same slide). Lateral view of two zoecia, showing an ovicell, two frontal avicularia, and the characteristic internal calcareous bars.



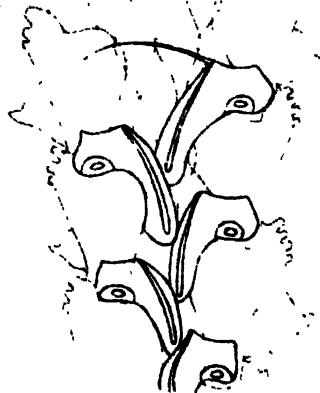




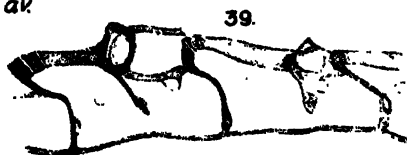
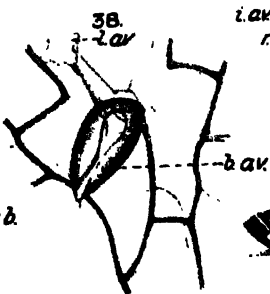
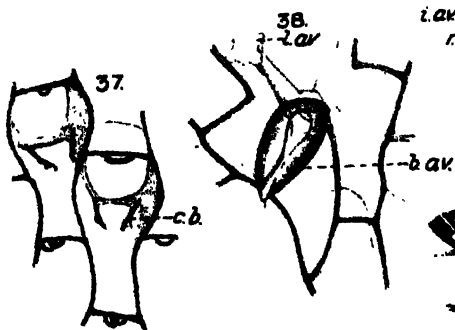
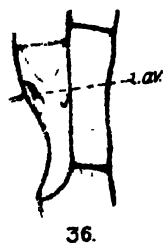
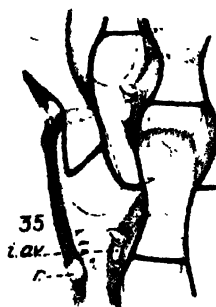
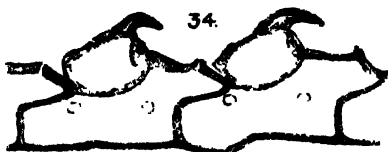
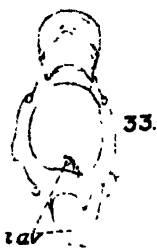
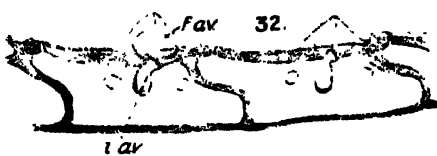
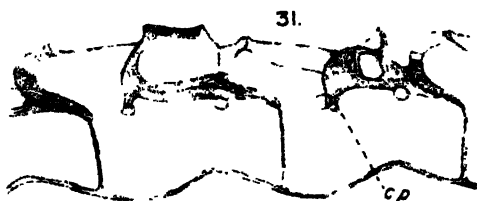
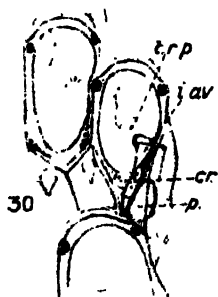
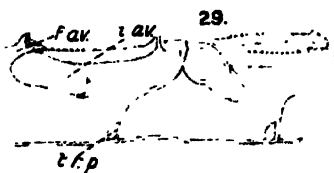
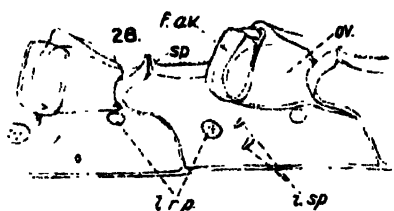
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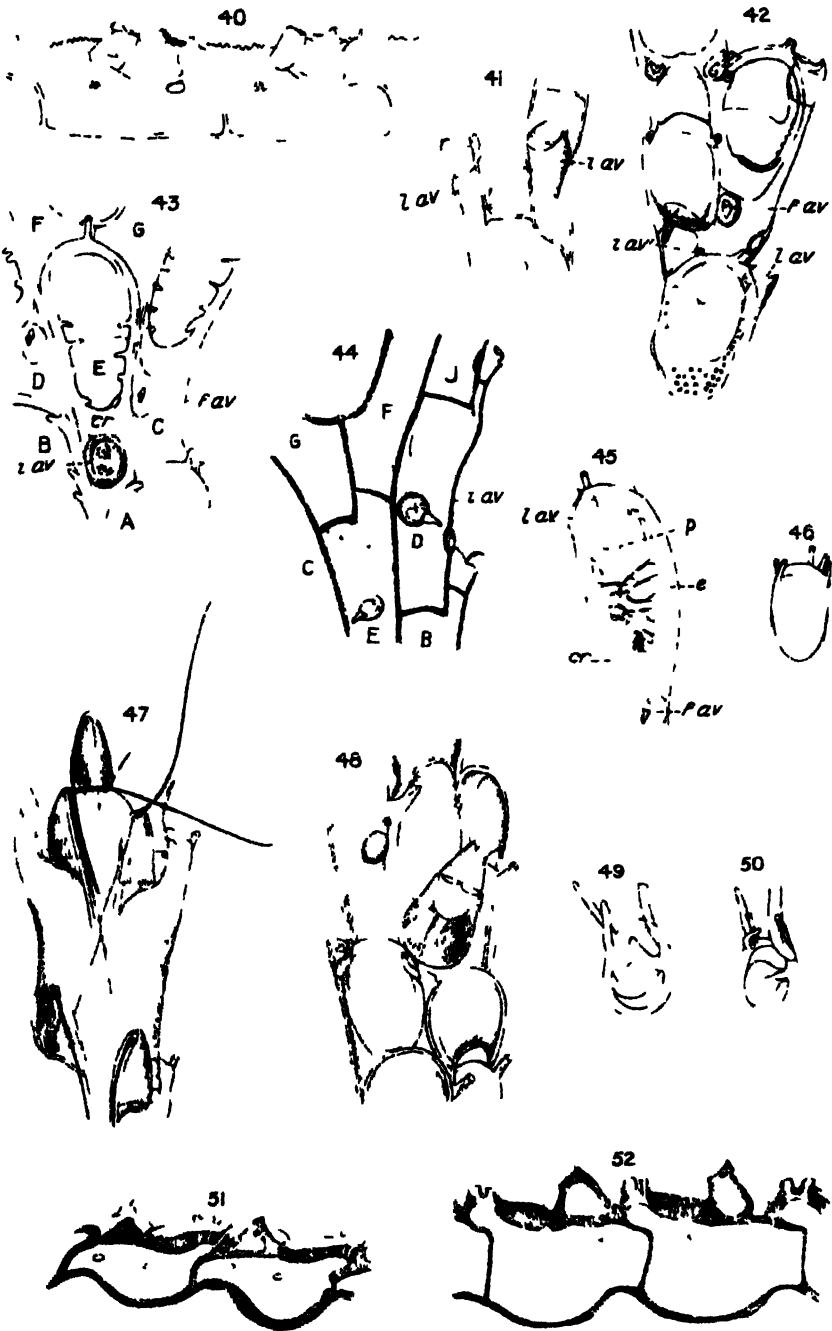














## PLATE 19.

The originals of Figs. 40-42, 51 and 52 were treated with Eau de Javelle.  
Scale of figures as in Pl. 18.

- Fig. 40.—*Menipea triseriata* (Simon's Bay, S. Africa, 'Challenger,' B.M. 87.12.9.99). Lateral view of two zoecia with ovicells and frontal avicularia.
- Fig. 41.—*Menipea triseriata* (same slide). Basal view, showing an internal avicularium (*i.av.*), a lateral avicularium (*l.av.*), and the origin of a marginal rootlet (*r.*).
- Fig. 42.—*Menipea triseriata*. Frontal view of the same zoecia; *f.av.* frontal avicularium; *i.av.*, internal avicularium; *l.av.*, lateral avicularium, above which is seen the origin of a rootlet.
- Fig. 43.—*Menipea marionensis* (Simon's Bay, 'Challenger,' B.M. 87.12.9.99). Frontal view: *cr.*, cryptocyst; *f.av.*, normal frontal avicularium; *i.av.*, base of an internal avicularium, showing the origin of its muscles from the frontal surface.
- Fig. 44.—*Menipea marionensis* (Cape of Good Hope, 'Challenger,' Stat. 142, B.M. 99.7.1.698). Basal view, showing two internal avicularia (*i.av.*), with their mandibles.
- Fig. 45.—*Menipea marionensis* (same slide as fig. 43). An old zoecium, showing an excessive development of the internal calcareous spines; *cr.*, cryptocyst; *p.*, proximal end of the next distal zoecium, connected with the edge of the opesia (*o.*) by a calcareous film; *f.av.*, frontal avicularium; *l.av.*, lateral avicularium.
- Fig. 46.—*Amastigia kirkpatricki* (Lev., MSS.), n. sp. (Marion Id., 'Challenger,' B.M. 87.12.9.97). Young zoecium, with 5 oral spines.
- Fig. 47.—*Amastigia kirkpatricki* (same slide). Basal view, showing vibracula, the uppermost axillary.
- Fig. 48.—*Amastigia kirkpatricki* (same slide). Frontal view, showing a gigantic frontal avicularium and two ovicells.
- Fig. 49.—*Amastigia rudis* (Victoria, B.M. 97.5.1.462). Part of a zoecium, with scutum, in frontal view.
- Fig. 50.—*Amastigia nuda* (Victoria, B.M. 97.5.1.246). A similar preparation, frontal view.
- Fig. 51.—*Amastigia nuda* (same slide as fig. 50). Lateral view of two zoecia, with frontal avicularia (paired).
- Fig. 52.—*Amastigia rudis* (same slide as fig. 49). A similar view of two zoecia with frontal avicularia.



Notes on Acari, with Descriptions of New Species. By J. N. HALBERT.  
M.R.I.A. (Communicated by Dr. W. T. CALMAN, F.R.S., Sec.L.S.)

(PLATES 20-22.)

[Read 1st March, 1923.]

WITH a few exceptions the Acari recorded in the following paper were collected in Ireland since the publication of the Clare Island Survey reports seven years ago. The list of Acari there recorded (23) was practically a complete one in so far as the Irish terrestrial forms were then known. A few years later an account was given of the species found living in the zones of the sea-shore affected by the tides (24). At the present time, collections are being made with the intention of preparing a more complete list of our Acarid fauna, but much remains to be done in this respect. Meanwhile it is desirable to record a certain number of new and interesting forms as a contribution to our knowledge of the Acari in these islands.

The literature dealing with the Acari is very considerable: large numbers of species have been described by European workers in recent years, and, as very many of these species are unfigured, the difficulties of identification are greatly increased. In the present paper short descriptions only are given, and such figures as seem necessary in a group where the details of structure are so varied and often of so comparative a character. In all, some sixty-eight species are recorded: sixteen of these, and also a few varieties, belonging to the families Gamasidae, Oribatidae and Trombididae, are apparently undescribed. Including these new forms, about forty species are now recorded for the first time from the Britannic area. The types of two of the new species, in *Lasioseius*, were collected by Mr. A. D. Michael on the coast of Cornwall some years ago.

I am indebted to a few friends for assistance in the collecting of specimens, more particularly to my colleague, Mr. A. W. Stelfox; the discovery of some of the more interesting forms is due to him. I have also to thank Dr. A. Berlese for kind help in the identification of some of the species: others are recorded on my own responsibility. The type-specimens of all the new species are in the collection of the Irish National Museum.

*GAMASUS* (*EUGAMASUS*) *CRASSITARSIS*, sp. nov. (Pl. 20. figs. 1  $\sigma$ -c.)

*Male*. A large robust species measuring  $1600\mu$  in length: general characters as in the subgenus *Eugamasus*, to which the species belongs. Shoulders well marked; hairs long, those on the second dorsal shield numerous and somewhat adpressed. Sternal region of ventral plate with faint scale-like markings on its anterior half, concave at the centre of the

front margin. Genital aperture strongly chitinized, posterior extremities pointed, reaching to middle of second coxæ. Epistome with a long central spine, and the ends of the lateral spines slope slightly inwards. Maxillary plate transverse, with four long hairs. Chelicerae (fig. 1 a) somewhat like those of *G. oudemansi*, Berl.; fixed chela armed with two stout teeth, the extremities of which are truncated and minutely dentate, apex of segment bilobed; free chela with one strong tooth slightly recurved.

First, third, and fourth legs long and slender; third segment of last pair with a sharply-pointed ventral spine. Second legs (fig. 1 b) very stout; femoral calcar of moderate size, curved posteriorly, bluntly pointed; cap of axillary process flattened and produced towards apex of calcar as in *G. oudemansi*, Berl.; on the outer side of the femur there is a marked chitinous prominence (fig. 1 c) with a terminal hair; genual process well developed, cap concave; process of fifth segment not prominent, its extremity does not project beyond the ventral outline of the segment. Tarsi strongly swollen at the base and again at the apex; a stout conical tooth stands near the middle of the inner surface.

This fine species is evidently allied to *Gamasus magnus*, Kramer, and to *G. oudemansi*, Berl. It is however larger, and differs from both in the presence of a chitinous projection on the outer side of the second femora; the tarsi and chelicerae are also different. It also resembles the species redescribed as "*Eugamasus loricatus*, Wankel" by Oudemans (38, p. 114), especially in the form of the tarsi, but differs from this species in the armature of the second legs and in other particulars.

*Locality.* Two males found under a sunken stone at high-tide mark in company with the local *Chelifer dubius* (Cumb.) at Mount Garrett Wood, near New Ross, Co. Wexford, by Mr. R. J. Phillips, 12th March, 1922.

**GAMASELLUS (PROTOLÆLAPS) GRANULATUS, sp. nov. (Pl. 20. figs. 2 a, b.)**

A very distinct species belonging to the subgenus *Protolaelaps*, Berlese (13, p. 137). It is remarkable for the comparatively large size of the ventral plates, more especially of those enclosing the peritreme. Verified by Dr. Berlese.

*Female.* Colour yellowish brown, shape pyriform. Cuticle very distinctly punctate-striate. The two dorsal plates are of equal breadth, leaving a rather wide uncovered lateral margin; the second plate is undulate in front and almost reaches end margin of body. These plates are minutely punctured, and there are faint traces of reticulate markings. Hair armature short and stout. Jugular plates absent. Sternum with a bow-shaped front margin, rather long, reaching middle of third coxæ; end margin truncate. Metasternal plates with a stout hair on outer margins. Genital plate sub-quadrangle (length  $75\mu$ ), anterior half lying between last pair of coxæ. Ventro-anal plate large, twice as broad as long (length  $100\mu$ , breadth  $200\mu$ );

front margin flattened, end bluntly pointed and reaching margin of body. All of these ventral plates are minutely punctured. Peritreme strongly sinuate, lying close to the legs on the inner margin of a large plate which projects in a broad tongue-shaped process beyond, but does not enclose, the last pair of legs. Rod-like endopodial plates lie between the third and fourth coxæ.

Epistome with a long central spine fringed with minute hairs. Maxillary plate quadrate; the small curved lobes are placed on a raised central part which projects beyond the front margin of the plate. (Chelicerae very minute. Palps normal. Legs robust, of moderate length, clothed with short hairs; ambulacra on all pairs. Length  $363\ \mu$ , breadth  $275\ \mu$ .)

*Locality.* Apparently a rare species; found on two occasions, in January and November, under stones in the Tolka Valley, near Dublin.

**GAMASELLUS (PROTOLÆLAPS) MUCRONATUS (G. et R. Can.).**

1881. *Gamasus mucronatus*, G. et R. Canestrini, 19, p. 1081.—1882. G. et R. Can., 20, p. 52.—1885. G. Can., 18, p. 78.—1887. *Cyrtolælaps mucronatus*, Berlese, 1, Fasc. xlv. n. 5.—1921. Berlese, 15, p. 81.

This species may be recognized by its large size, measuring  $1200\ \mu$  in length, and the large strongly-chitinized dorsal plates. In addition to a number of minute hairs, both plates carry two pairs of strong spines feathered at their extremities; one pair at the end of the second plate project well beyond the posterior margin of the body. The peritreme lies close to the coxæ on the inner margin of a large peritrematic plate. The ventro-anal plate is large, V-shaped, emarginate in front, its extremities lying close to the genital plate and the posterior margin of the body.

*Locality.* Females found in rotting potatoes at Drumcondra, near Dublin, in April. The identification has been verified by Dr. Berlese, who refers (*in lit.*) the species to his subgenus *Protolælaps*. The male has not been described.

**GAMASELLUS (PROTOLÆLAPS) SUBNUDUS?, Berl. (Pl. 20. fig. 3.)**

1918. Berlese, 13, p. 138.

The following is a brief description of a *Gamasellus*, as well as of its larva and nymph, which probably belongs to the present species, although the identification is given with some reserve.

*Adult female* pear-shaped. Epistome with a long sinuate spine, minutely spiculate at the base. Dorsal shields of moderate size and uniform breadth, distinctly punctate, the punctures lying in transverse rows; margin of second shield broken up into small folds, and there is a wedge-shaped fissure in the middle of the front margin; hairs sparse and weak. Epidermis strongly granulate. Sternum of moderate size (length  $132\ \mu$ ), hinder corners slightly rounded. Endopodial plates very strongly developed and



produced in sharply-pointed processes between the coxæ. Peritreme undulate, and protected by a narrow plate which reaches to the end of the fourth coxæ. Ventro-anal shield very small, rotund, broader than long (breadth  $165\ \mu$ ), placed on the posterior margin of the body. Legs of moderate length, second pair slightly more robust than the two hinder pairs. Length  $742\ \mu$ , breadth at shoulders  $430\ \mu$ , and in posterior third of body  $512\ \mu$ .

*Larva*. Shape much as in adult; close to the end it slopes rapidly to a truncated central part of the posterior margin, at each corner of which is a curved hair; immediately behind these on each side are stouter hairs with slightly clubbed and spiculate extremities; the dorsal hairs are weak. Dorsal shields undeveloped, and the epidermis at end of body is distinctly areolated. Legs and palps very stout, carrying numerous short hairs; ambulacra consisting of a single pair of rather narrow leaf-like upper lobes, and two long, lanceolate, lower processes. Length  $340\ \mu$ , breadth  $198\ \mu$ . (Pl. 20. fig. 3.)

*Nymph*. Side margins more parallel than in the adult; end margin truncated, with a small central part projecting below. Dorsal plates large, granular. Side margins of body with short hairs. Epistome, palps, and legs much as in the adult. Length  $570\ \mu$ , breadth  $320\ \mu$ .

*Locality*. Adult female, larva, and nymph found in decaying turnips, North Dublin, in April 1921.

#### MACROCHELES VAGABUNDUS (Berl.).

1889. *Holostaspis vagabundus*, Berlese, 1, Fasc. lii. n. 8.—1902. Oudemans, 37, pp. 11, 43.—1918. Berlese, 13, p. 172.

Berlese places this species in the subgenus *Macrocheles* (*sensu stricto*, 13) of which the type is *Acarus marginatus*, Hermann. In the same paper he records varieties of *M. vagabundus* from South America, South Africa, and Australia, so that the species is of unusually wide range. It may be known by the beautiful sculpturing of the dorsum, which, as well as being distinctly punctured, is ornamented with reticulations and branched chitinous markings on the epidermis. The strong, curved hairs on the margin of the dorsal plate bear numerous very short secondary hairs.

*Locality*. The only specimens ( $\varnothing\ \varnothing$ , length  $930\ \mu$ ) found in Ireland were under moist pieces of wood lying on the sea-bank at Malahide, Co. Dublin, in September.

#### DENDROLAPUS CORNUTUS (Kramer).

1886. *Seius cornutus*, Kramer, 31, p. 257.—*Dendrolaps bicornis*, Hull, 25, p. 67.

This species is well described and figured by Kramer (31), and is easily recognized by the presence of two long chitinous horns near the end of the dorsum in the male. In the female (length about  $495\ \mu$ ) the body is rather long and narrow. The sternum fills the entire space between the very large second coxæ, and is gradually widened to its hinder corners. The genital

and ventro-anal shields are remarkably long and narrow, of almost equal breadth, and the latter reaches to within a short distance of the end margin of the body.

*Locality.* Both sexes occurred under the moist bark of cut pine-logs lying on the Royal Canal bank, close to Dublin, in October 1918. The logs had been brought from an inland locality.

**MYONYSSUS DECUMANUS, Tirabosche.**

A few adult females were found on a Field Mouse (*Mus sylvestris*) caught in the Rocky Valley, Co. Wicklow, by Dr. R. F. Scharff. On the same host were adults of *Laelaps stabulasis*, C. L. Koch, and *L. agilis*, C. L. Koch. It has been found on the common Brown Rat in England (Hull, 25), and Waterston records its occurrence on the House Mouse in the Shetland Islands.

**ANTENNOPHORUS UHLMANNI, Haller.**

A single specimen was found in a nest of the ant, *Lasius mixtus*, Nyl., near Graiguenamanagh, in Co. Kilkenny, by Mr. A. W. Stelfox. This is the only *Antennophorus* hitherto found in Ireland; all the described species, four in number, have been recorded from England.

**LÆLAPS (IPHIS) ACULEIFER, Can.**

1883. *Laelaps aculeifer*, Canestrini, 17, p. 6.—1885. *Hypoaspis aculeifer*, Canestrini, 18, p. 84.—1892. *Laelaps aculeifer*, Berlese, 1, Fasc. lxviii. n. 10.

Evidently a fairly common species. I have found the female in numbers under bark of decayed trees at Tallaght in April and Greystones in July, under pieces of damp wood in the Tolka Valley in January, and in decayed potatoes at Drumcondra in April. All these localities are in the vicinity of Dublin.

**LÆLAPS LATISTERNUS, sp. nov. (Pl. 20. fig. 4.)**

*Female.* Shape broadly ovate, shoulders not prominent. Dorsal plate very large, surface with scale-like markings; hairs short, becoming longer towards end margin, where there are two comparatively long hairs. Sternum very wide and strongly produced between the coxæ at its anterior and posterior corners, end margins slightly undulate, hairs rather long. The genital plate is also rather large (length about  $165\mu$ ), marked with lines as in figure. Peritreme comparatively straight, not fused with the pedal plates; the latter are well developed and enclose the fourth coxæ; small obliquely-placed inguinal plates lie close to them. Ventro-anal plate small (length  $220\mu$ , breadth  $176\mu$ ), subovate, flattened at end and reaching margin of body.

Epistome in the form of a long, sword-shaped, central spine and two strong lateral teeth. Maxillary plate rather narrow ( $77\mu$ ). Palps normal. Legs long and robust, first pair of very uniform thickness (length about  $506\mu$ ); the fourth pair (length  $550\mu$ ) have slightly curved femora, and the tarsi are elongate; there are traces of a division of the terminal part of the tarsus close

to the middle. Hair armature short, that of first pair stronger than the others. Ambulacra normal. Length  $530\ \mu$ .

*Locality.* Found under stones in the Lucan Demesne, Co. Dublin, February.

*LÆLAPS SIMPLEX*, sp. nov. (Pl. 20. fig. 5.)

*Female.* Long oval, shoulders not well marked. Dorsal plate straight-sided, reaching end of body, with three double rows of weak hairs, two on the posterior margin much longer. Epidermis distinctly striated. Sternum of rather uniform breadth, reaching to middle of third coxæ; front margin undulate, with slight lateral extensions; posterior corners pointed; end margin with a small notch at the middle; the three pairs of hairs are placed close to the margin of the shield. Genital plate exceptionally long (length  $110\ \mu$ ) and narrow, being more than twice as long as broad, reaching well beyond the last pair of coxæ, only slightly widened at the extremity, which is somewhat rounded. Ventro-anal plate small (length  $90\ \mu$ , breadth  $95\ \mu$ ), widely removed from genital plate and placed on the end margin of the body, evenly rounded in front and truncated behind. A pair of small inguinal plates lie near the side margins. The inner pedal plates lie between the last pair of coxæ, which are partly enclosed by a chitinous extension of the peritreme. Chelicerae small, though of robust structure. Legs and palps stout and of moderate length; inner side of second palp segment with one, and third segment with two stout spines. Length  $450\ \mu$ , breadth  $260\ \mu$ .

*Locality.* Taken under rotten wood at Glendalough, Co. Wicklow, in September.

*LÆLAPS FIMBRIATUS*, sp. nov. (Pl. 20. fig. 6.)

*Female.* Long oval. Dorsal plate rather narrow; hairs long, increasing a little in length at end of plate. Sternum rather short; front margin bow-shaped, extending between the coxæ; sides deeply emarginate. Metasternal hairs present, but the plates are indistinct. Genital plate large (length about  $150\ \mu$  along middle line), elongate, constricted at the middle; front margin produced and elaborately fimbriate, hind margin straight; anterior part of plate marked with longitudinal lines. Ventro-anal plate large (length  $175\ \mu$ , breadth  $150\ \mu$ ), hatchet-shaped, the bluntly-pointed end directed towards the posterior margin of body; surface with transverse lines; front margin much wider than genital plate. The outline of the plate of an earlier nymphal form is indicated in the drawing. Peritreme with a slight regular curve; there is no protecting plate, and a weakly-chitinated post-stigmatic process encloses the last pair of coxæ. Maxillary plate quadrate, corniculi narrow and placed close together. Legs long and slender (length of first pair  $450\ \mu$ , of fourth pair  $550\ \mu$ ). Ambulacra rather long and narrow, but otherwise of normal structure. Length  $528\ \mu$ , breadth  $320\ \mu$ .

*Locality.* Found on sprouting potatoes at North Dublin in March of the present year.

*COPRIPHIS (ALLIPHIS) HALLERI (G. et R. Can.).*

1881. *Gamasus halleri*, G. et R. Canestrini, 19, p. 1077.—1882. *Laelaps halleri*, G. Canestrini, 20, p. 57.—1885-'99. *Iphis halleri*, G. Canestrini, 18, p. 93.—1892. *Iphis halleri*, Berlese, 1, Fasc. lxxvii. n. 6.

*Localities.* Males and females occurred commonly in decayed roots of Henbane at Clontarf, near Dublin, in August 1918, and under bark of cut pine-logs on the Royal Canal bank in October 1918. Canestrini records it as occurring in decayed potatoes and amongst rotting leaves in December.

*LASIOSEIUS (LASIOS.) GRACILIS, sp. nov. (Pl. 20. figs. 7 a-c.)*

*Female.* Shape ovate, shoulders not marked. Dorsal plate large, almost completely covering body, surface with polygonal markings. Hairs long, formed of a strong rib and blade, curved and serrulate, those on end margin exceptionally so (length  $65\mu$ ). Frontal bristles shorter and strongly pectinate. Sternum of moderate size, corners not produced between the coxæ; hinder margin straight, with rounded corners about on a level with end of second coxæ. Metasterna small. Genital shield broad posteriorly and rather strongly narrowed towards the front; lying behind it are two thin chitinous bars and two pairs of hairs. Ventro-anal plate of medium size, a little broader than long (length  $145\mu$ , breadth  $150\mu$ ), flattened in front and regularly rounded behind. Anal aperture placed a little in advance of the centre of the plate. Inguinal plates linear, placed near side margins. Maxillary plate transverse, evenly rounded at base; corniculi with their apices trifid, directed inwards, and there is a strong hair at their bases. Chelicerae small; fixed limb swollen at the base, where there are four sharply-pointed teeth placed close together; free chela with an oblique chitinous blade and traces of two or three teeth just before the apex. Palps normal. Legs of moderate length, rather slender, furnished with short, curved hairs, some of which are minutely spiculate; length of first leg about  $352\mu$ , of fourth leg  $363\mu$ , not including ambulacra. Length  $474\mu$ , breadth  $310\mu$ .

Dr. Oudemans has partially described (37, p. 17) the protonymph, deutonymph, and adult of an Acarid which he calls *Seiulus plumosus*, though it seems doubtful if all of the forms are referable to the same species. *L. gracilis* is allied to "*Seiulus plumosus*," but the legs are obviously longer and more slender, and the hairs of the dorsum are much longer and not so strongly blade-shaped as they are in the Dutch species, which was found on a bat (*Vespertilio dasycneme*) and on a Squirrel (*Sciurus vulgaris*).

*Locality.* Found on sprouting potatoes at the Albert Model Farm, near Dublin, by Mr. J. G. Rhynehart, early in March.

*LASIOSEIUS* (*LASIOS.*) *OMETES*, *Oudem.* (Pl. 20. figs. 8 a-c.)

A *Lasioseius* found under the bark of trees in Ireland seems referable to this species. I have to thank Dr. Oudemans for kindly lending me his type-specimen for comparison.

Form as in *L. muricatus*, C. L. Koch (Berlese, 1, Fasc. xli. n. 6). Sternum with a wide and deep cleft in the posterior margin extending to about the middle of the plate; the sides of the cleft are usually irregular in outline. Metapodial plates vestigial. Genital plate of the usual shape, punctured; end margin rather strongly chitinized; immediately behind it are four small linear plates arranged in a transverse row. Ventro-anal plate very large, with distinct transverse markings; side margins concave towards apex; the end margin is somewhat truncated, and reaches the posterior margin of the body. The peritreme is normal, and its plate is continuous with the inner pedal plate, the extremity of which reaches the third coxae. Tritosternum with rather short processes; its base lies in the central depression of the bow-shaped jugular bar. Fixed chela with a row of about ten small teeth, and there are three teeth on the free chela (fig. 8 c). Legs, palps, and capitulum much as in *L. muricatus*, C. L. Koch. Length 580  $\mu$ ; breadth 319  $\mu$ .

*Localities.* Females found under bark of decayed logs at Tallaght, and in the Carton Demesne, Co. Kildare, in May.—(See note on p. 392.)

*LASIOSEIUS* (*LASIOS.*) *LÆLAPTOIDES* (*Berl.*)

1887. *Epicrius lælaptoides*, Berlese, 1, Fasc. xl. n. 10.—1916. Berlese, 10, p. 33.—1921. Berlese, 15, p. 82.

*Locality.* Female found under damp wood lying on the ground in the Tolka Valley, near Finglas, Co. Dublin, in May. Not previously recorded from Britain.

*LASIOSEIUS* (*EPISEIUS*) *GLABER*, *Berl.*, var. *CURTIPES*, nov. (Pl. 20. fig. 9.)

General structure as in the type-form (Berlese, 1, Fasc. xxx. n. 9); differs in the much shorter first pair of legs; in his description of these, Berlese says: "antici exiliiores, corpore fere duplo longiores," and his accompanying figure shows the first legs much longer than the body. In the present variety the first legs are only slightly longer than the body, and the remaining pairs are somewhat stouter. The ambulacra are of the modified, bristle-like type. The genital plate is longer and the ventro-anal plate is broader. Trägårdh has described a variety (*minor*, Träg., 46, p. 432) found in the Sarekgebirge; from this the present variety may be known by the more strongly-produced metapodia, and the form of the ventral plates is different.

*Female.* Dorsum with scale-like markings, which are distinct only towards the margins. Hair armature weak, stronger towards end margin, on which

are a number of very short spines. Sternum rather large (length  $187\ \mu$ , breadth  $165\ \mu$ ). Jugularia absent. Metasternal plates extremely small. Genital plate longer than broad, with a thick hinder margin. Metapodial plate much produced, and ending in a bluntly-pointed extremity reaching beyond the front margin of the ventro-anal plate. The latter is large and much broader than long (length  $120\ \mu$ , breadth  $154\ \mu$ ), front margin truncated, posterior margin evenly rounded. Inguinal plates inconspicuous. Length  $429\ \mu$ , breadth  $252\ \mu$ .

*Locality.* Two specimens found amongst wet moss collected on Lambay Island, Co. Dublin, in July.

*LASIOSEIUS (EPISEIUS) SPHAGNI*, sp. nov. (Pl. 20. fig. 10.)

This species bears a superficial resemblance, especially in the form of the ventral plates, to *L. helaptoides*, Berl., but, apart from other differences, it may be easily known by the elongate tarsi and modified ambulacra, which are of the *Episeius* type, with long terminal bristles, while in *L. helaptoides* these parts are of the ordinary *L. muricatus* type.

*Female.* Colour light brown, shape broadly ovate. Dorsal plate very large, surface not reticulate, but with indistinct areolations on its anterior part. Hair armature weak, a row on side margins stronger, and there are three pairs of deflexed hairs on the end margins. Jugular plates absent. Sternum normal (length  $110\ \mu$ ). Metasternalia distinct. Genital plate broad, front margin indistinctly serrulate: lying behind this plate are four small linear plates. Ventro-anal plate large, broader than long (length about  $200\ \mu$ , breadth  $264\ \mu$ ), front margin flattened. Sides produced in a rounded prominence in front, emarginate towards apex, which is somewhat truncated and minutely punctured. Canal of peritreme broad, with the usual post-stigmatic continuation, and protected by a narrow outer plate. Metapodia strongly chitinized, ending in bluntly-pointed extremities, much as in *L. italicus*, Berl. Epistome tricuspid. Maxillary plate quadrate; corniculi small and slightly sinuate, and three pairs of long hairs stand near their bases. Palps normal. Legs long and robust; length of first and fourth pairs about equal ( $562\ \mu$ ); ambulacra with three terminal bristles and a pair of small membranous lobes.

*Locality.* Two specimens found in sphagnum collected in the Black Valley, Howth, Co. Dublin, in October.

*LASIOSEIUS (EPISEIUS) ITALICUS*, Berl., L. (E.) *MICHAELI*, sp. nov.,  
L. (E.) *TENUIPES*, Halbt., and L. (E.) *MAJOR*, sp. nov.

From a study of the species belonging to the "*italicus*" group of the subgenus *Episeius*, Hull, which includes those species of *Lasioseius* in which the tarsi are elongate and the ambulacra armed with bristles instead of the usual

lobes (Hull, 25 ; Halbert, 23, 24), I believe there are at least four closely-allied species in these countries. The male and female of three of these are now known to me, and although the general structure is much alike, the males possess excellent characters in the form of the mandibular calcar. These three species are *L. (E.) italicus*, Berl., *L. (E.) michaeli*, sp. nov., and *L. (E.) major*, sp. nov. The male of *L. (E.) tenuipes*, Halbt., has not been discovered, and until this is found I must rely on the characters of the single specimen described (23, p. 78). The females in the case of two of the species, i. e. *L. (E.) italicus* and *L. (E.) michaeli*, are difficult to separate; indeed, the one description would suit both species almost equally well. Unfortunately the males, as in many Acarid genera, are decidedly rare; as an instance, I may mention that out of a gathering from one locality of about one hundred examples of "*italicus*" aggregate three males were found, and this only by close searching of moss brought home from a suitable locality. The species frequent wet moss, liverworts, &c., and may be found amongst submerged mosses growing on stones in mountain-streams, in company with mites of the genera *Calonyx*, *Paniscus*, and *Aturus*.

The female of *L. (E.) italicus*, Berl., is described in 4, p. 234, and is excellently figured by Dr. Berlese in a later paper ("Redia," vi. pl. 19. fig. 35), while the male is briefly described in 10, p. 34. In view of the great similarity of the females of these species, it will probably be sufficient to give a short description of *L. (E.) italicus*, and then briefly tabulate the chief characters of the four species. Figures of the male mandibular calcars of three species and of the female of *L. (E.) major*, sp. nov., are given in the present paper.

*L. (E.) italicus*, Berl. *Female*. Shape pyriform. Dorsal shield large, reaching end of body; sides often slightly rounded, surface reticulate. Hair armature weak on centre of dorsum, much stronger and somewhat adpressed at the margins, where they are arranged in a double row. There is a raised tubercle near the posterior margin. Epistome of the tricuspid *Episcius* type. Sternum rather large and wide; both the front and hinder margins are slightly concave, and the latter reaches to middle of the third coxæ. Genital plate hatchet-shaped; hinder margin straight, standing well beyond the fourth coxæ. Ventro-anal plate large, much broader than long (length 210  $\mu$ , breadth 300  $\mu$ ), flattened in front; side margins concave near centre, surface with irregular lozenge-shaped markings. Between the last two plates are three pairs of very minute plates arranged in two rows. Peritreme broad and strongly sinuate. The united plates of the peritreme and metapodia extend beyond the last pair of coxæ in an obtusely-pointed triangular form. Legs very long, with attenuated tarsi, and the ambulacra have bristle-like lateral lobes and a lanceolate upper lobe. Length about 640  $\mu$ , breadth 420  $\mu$ .

## I. A raised tubercle present near end of dorsum in both sexes.\*

A. The extremities of the metapodial plates slope downwards in an oblique line towards the body margins.

- a. Male: Length 495  $\mu$ , breadth 330  $\mu$ . Calcar of mandible (Pl. 20. fig. 11) long, consisting of a thickened rib and narrow blade, flagelliform, curved strongly downwards under the maxillary plate, extremity sinuate. Female: Length 640  $\mu$ , breadth 420  $\mu$ ; body usually broader and more rounded than in the following species. Length of first leg 716  $\mu$ , of fourth leg 768  $\mu$ . (Localities: Streams at Glencullen, Glencree, Kilmashogue, in the Dublin Mountains; Reservoir at Greystones, July. Lambay Island, July, &c.)

*Lasioseius (Episeius) italicus*, Berl.

- b. Male: Length 495  $\mu$ , breadth 330  $\mu$ . Calcar of mandible (fig. 12) long (length about 210  $\mu$ , not including base of mandible), almost straight except at the apex, where it is deflexed. Length of first leg 470  $\mu$ , length of fourth leg 614  $\mu$ . Female: Length of type 640  $\mu$ , breadth 390  $\mu$ ; length of first leg 692  $\mu$ ; length of fourth leg 768  $\mu$ . (Locality: Mill Bay, Land's End, England; taken by Mr. A. D. Michael in November 1892.)

*Lasioseius (Episeius) michaeli*, sp. nov.

B. Extremities of metapodial plates truncated, lying in a straight line across the venter. Male unknown. Female described in 23, p. 78. Length about 740  $\mu$ , breadth 486  $\mu$ . Length of first leg 742  $\mu$ , of fourth leg 820  $\mu$ , including ambulacra. (Locality: Mountain-stream near Glencree, May.)

*Lasioseius (Episeius) tenuipes*, Halbt.

## II. No tubercle at end of dorsum.

Male: Length 520  $\mu$ , breadth 374  $\mu$ . Calcar of mandible (fig. 13 b) short (length about 70  $\mu$ , not including base of mandible), straight, or slightly curved; apex deflexed. Female (fig. 13 a), length 740  $\mu$ , breadth 486  $\mu$ . Body broadly pyriform, posterior margin somewhat flattened. Ventro-anal plate large (length 220  $\mu$ , breadth 336  $\mu$ ), distinctly reticulate. Length of first leg 820  $\mu$ , of fourth leg 890  $\mu$ . (Localities: Streams at Kilmashogue ( $\sigma$  &  $\varphi$ , December) and Glencullen ( $\varphi$   $\varphi$ , October), Mill Bay, Land's End, England ( $\sigma$  &  $\varphi$ , November, coll. A. D. Michael).)

*Lasioseius (Episeius) major*, sp. nov.

## LASIOSEIUS (PLATYSEIUS) SUBGLABER (Oudem.). (Pl. 20. fig. 14.)

1906. *Hypoaspis subglabra*, Oudemans, 36, p. 88.

A very distinct species, evidently referable to the subgenus *Platyseius*, Berlese (10, p. 42). Characteristic features are the broad pyriform shape and the very long hairs fringing the side margins of the dorsal shield. These hairs are arranged in an irregular double row and are incurved; on the end margin are two shorter, straight hairs. Length 560–600  $\mu$ , breadth 430  $\mu$ . Length of first leg 666  $\mu$ , of fourth leg 717  $\mu$ .

\* The male of *L. (E.) tenuipes* is unknown. In a recent paper on Swiss Acari, Dr. Schweizer described and figured what he considers is the male of *E. tenuipes*, Halbt. (41, p. 43). I was struck by the similarity of the male calcar there figured with that of *L. (E.) major* now described. Dr. Schweizer very kindly sent me some mounted specimens ( $\varphi$   $\varphi$ ) for examination (locality, Quellen am Kellersee, 4. iv. 1819) and they are undoubtedly referable to this species. The male calcar figured (Pl. 21. fig. 18) agrees well with that of my type of *L. (E.) major*.



The male of this species has not been described. The general structure resembles the males of *Episeius*. Dorsum as in the female. Free chela (fig. 14) armed with a long process resembling that of *L. (E.) italicus*, Berl., but shorter and less curved, each chela with one strong tooth, in front of the tooth on the fixed chela is a row of very small teeth. Length of male 484  $\mu$ , breadth 352  $\mu$ .

On account of the apparent difference in the length of the dorsal hairs in the Irish specimens when compared with the published figures (36, Taf. 6. fig. 45), I sent drawings to Dr. Oudemans, who informs me that they undoubtedly represent *L. (P.) subglaber*. The dorsum of this species is frequently coated with fragments of debris which are entangled between the long inwardly-curved marginal hairs, reminding one of what occurs in the Oribatid genus *Damareus*.

*Localities.* In sphagnum pools at Lough Atorick, Co. Clare, June, and also at Lough Dan, August. Both sexes occurred amongst wet moss collected on the bank of a stream at Glencullen in the Dublin Mountains, in October, and at Drogheda in August.

*LASIOSEIUS (LEIOSEIUS) MINUTUS (Halbt.).*

1915. *Seiulus minutus*, Halbert, 23, p. 76.—1918. *Zerconopsis minutus*, Hull, 25, p. 93.

—1920. *Lasioseius minutus*, Berlese, 14, p. 171.

Hull has placed the present species in a new genus *Zerconopsis*, of which the type is Kramer's "*Gamasus remiger*." Berlese, however, had already referred this species to his subgenus *Zercoseius* (10, p. 33) with *S. spathuliger*, Leon., as the type. On re-examining the Irish specimens of *L. minutus*, it seems to me they fall readily into Dr. Berlese's subgenus *Leioseius*, briefly diagnosed by him as follows:—"Ex gen. *Lasioseius*. Pedes breves et robusti. Truncus elongatus, lateralibus subparallelus. Typus *L. L. minusculus*, Berl." An estuarine species (*L. salinus*, Halbt.) of this subgenus occurs on the Dublin coast (24, p. 125).

*Localities.* Amongst sphagnum collected on Croaghmore Mountain, Clare Island, Co. Mayo, and under rotten wood lying on the ground in the Carton Demesne, Co. Kildare, May. The male is unknown.

*SEIUS TOGATUS*, (C. *L. Koch*).

Until recently (1916) acarologists referred species of very different facies to Koch's genus *Seius*. Many new genera and subgenera have now been established by Dr. Berlese, so that a great advance has been made. As *S. togatus* is the first species of the genus described by Koch it remains as the type. It is also a very isolated form with but few congeners; three have been described from Europe (see Berlese, 11, p. 150).

*Locality.* A single specimen found by Mr. Norman Stephens under the moist bark of a pine-stump at the entrance to The Devil's Glen, Co. Wicklow,

in May. The species has been recorded from Scandinavia (Trägårdh), Germany (Koch), Switzerland (Schweizer), and the North of England (Hull).

*ZERCON TRAGARDHI*, sp. nov. (Pl. 21. figs. 15 a, b.)

*Female.* Colour pale brown. Shape broad ovate. Side margins strongly serrated, and the end margin is crenulate much as in *Z. trigonus*, Berl. First dorsal shield sculptured with scale-like markings, second shield with areolations and four crescentic pore-like markings as in *Z. triangularis*, Koch; both shields have a double row of irregularly-shaped pits. The hair armature is characteristic; on the side margins there are ten pairs, not including the frontal spines, of strongly plumose hairs (fig. 15 b). The dorsal surface also carries a number of spines which are less strongly plumose than those of the margins; short spines spring from the marginal serrations. Sternum and genital plate of normal shape and rather weakly chitinated. Ventro-anal plate large, elliptical, though somewhat flattened on the front margin, with a few plain hairs. Legs robust and armed with plain spines, those on the middle segments of the first pair are somewhat stronger and are carried on distinct tubercles. Length 340  $\mu$ , breadth 250  $\mu$ .

This species is allied to *Z. ornatus*, Berl. (3); the body is relatively narrower, and the sides less strongly rounded, the margins are more distinctly serrated and carry fewer plumose spines. The last-mentioned character also separates it from *Z. radiatus*, Berl. (7, p. 9), in which the spines are more numerous.

*Locality.* Female found at roots of decayed Henbane plants in August.

*ZERCON PERFORATULUS*, Berl.

1904. Berlese, 3, p. 269.—1914. Berlese, 9, p. 136.

Originally described as a variety of *Z. triangularis*, C. L. Koch, and later raised to specific rank. Easily distinguished by the marking of the dorsal shields. In *Z. triangularis* these bear scale-like markings, while in the present species the markings are largely replaced, more especially on the second shield, by distinct punctures, and the hair armature also is weaker.

*Localities.* Glendalough, Co. Wicklow, found under chips of wood lying on the ground, April; Knappagh Wood, Co. Mayo, in moss, August, in company with *Z. triangularis* in both localities.

*CERATOZERCON BICORNIS* (Can. et Fanzago). (Pl. 21. fig. 16.)

1877. *Seius bicornis*, Canestrini et Fanzago, 21, p. 103.—1881. *Gamasus bicornis*, Kramer, 29, p. 14.—1882. *Laelaps bicornis*, G. et R. Canestrini, 20, p. 78.—1885. *Sejus bicornis*, Canestrini, 19, p. 91.—1887. *Zercon bicornis*, Berlese, 1, Fasc. xli. n. 8.—1910. Berlese, 7, p. 346.

This species has been described and figured as having only one plumose spine on the two chitinous horns of the posterior margin. Instead of this, in

the Irish specimen (length 342  $\mu$ , breadth 220  $\mu$ ), there are two plain spines (fig. 16), the outer one being a little longer than the other. It is possible, however, that the specimen may be immature. Canestrini remarks: "le quali portano all'apice, nelle forme giovani, ciascuna due setole, nelle piu avonzzate di età ciascuna una setola robusta diretta in dietro e in dentro" (20).

*Locality.* One female found under a stone on the Malahide sandhills in August.

*POLYASPINUS CYLINDRICUS*, Berl. (Pl. 21. fig. 17.)

1916. Berlese, 11, p. 134.—1917 Berlese, 16, p. 10.

This interesting genus was founded to receive the present species, and belongs to the tribe Polyaspidini of Berlese's recent classification of the family Uropodidæ (16). The species may be recognized by the elongate sub-parallel shape; the central area of the dorsum is protected by a long, narrow shield, smooth at the centre, roughened at the sides; at the end of this are three small shields, of which the middle one is the least, arranged in a transverse row. The marginal shields are represented by a row of small hair-bearing plates, and on the actual body margin are numerous similar plates. The venter is protected by strongly-chitinized and fused plates; their margins are indicated by thickened ridges. Peritreme placed on the side margins of the body. Hairs simple and blade-shaped. Legs robust, claws of the first pair much reduced. Length about 670  $\mu$ , breadth 300  $\mu$ . The male is unknown. Identification verified by Dr. Berlese.

*Locality.* Several females found under logs of wood half buried in the mossy banks of the stream between Glendalough and Laragh, in April.

*TRACHYTES PYRIFORMIS* (Kramer).

1876 *Trachynotus pyriformis*, Kramer, 28, p. 80—1877 Canestrini et Fanzago, 21, p. 68.—1882. Kramer, 30, p. 420. - 1892. *Trachynotus agrotæ* var. *pyriformis*, Berlese, 1 (Moscog. Supp. p. 94)—1894 Michael, 33, p. 313 1915 Berlese, 9, p. 134.

The above are the principal records undoubtedly referring to Kramer's species, which was described in 1876. There has been confusion between this species and the form described as *T. agrotæ* by Koch, and if the latter were clearly recognizable it would be the type of the genus *Trachytes*. There is doubt, however, concerning the identity of Koch's *T. agrotæ*, a species supposed to be the same was described and figured by Dr. Berlese (1, Fasc. xxxviii. n. 10), but he has since suppressed this, stating that it may have been identical with either of his two recently described species, *T. lambda* or *T. tubifer* (9, p. 135). It would then follow that *T. pyriformis*, Kramer, is the type of the genus *Trachytes*. Fortunately this species was carefully described and figured by Kramer (28). Mr. A. D. Michael has recorded both *T. agrotæ*, Koch, and *T. pyriformis*, Kramer, from English localities, but he did not describe the first-mentioned form.

*Locality.* Several females were found under branches and pieces of wood lying on the river bank at Glendalough in April.

*TRACHYTES* PI, *Berl.*, var. *PAUPERIOR*, *Berl.*

1915. *Berlese*, 9, p. 135.

Differs from the typical form (7) in its paler colour, smaller size, and in the form of the epigynum which is more elongate and punctured. The length of the Irish specimen is  $484\mu$ , breadth  $286\mu$ . Evidently closely allied to *T. minima*, Trüg. (44, p. 448), but in the present form the anterior part of the body is much more elongate and the shoulders are less marked.

*Locality.* A single female found under decayed wood at Poulanass, Glendalough, in April.

*UROSEIUS ACUMINATUS*, *C. L. Koch.*

*Locality.* A few specimens were found in company with numbers of *Uropodu obscura*, C. L. Koch, in decaying potatoes, Rocky Valley, Co. Wicklow, September 1921. The species has been recorded from Italy, Switzerland, Germany, and Great Britain. Hull queries the "*Cilliba vegetans*" of (25) as the present species, but the nymph recorded as such can have no relationship with *Uroseius*. The adult form of the "*Cilliba vegetans*" of authors has not been made known.

*DINYCHUS (PRODINYCHUS) CARINATUS*, *Berl.*

1903. *Berlese*, 3, p. 247.

This species is briefly described in the above reference, and it is not figured; Dr. Berlese, who has kindly verified the identification, refers the species (*in lit.*) to his subgenus *Prodinychus*. The size is rather small for this genus (length of Irish specimens  $622\mu$ , breadth  $333\mu$ ); shape of main body a regular oval, anterior part rather acutely pointed. In the middle line of the body there are two carinæ, and between these and the slightly raised lateral margins the dorsum is concave.

*Locality.* I have found this distinct species in two localities in Co. Dublin, once in decayed bulbs in January, and under bark of old moss-grown tree trunks at Lucan in April.

*PHAELOCYLLIBA VIRGATA* (*Hull*).

1918. *Cillibano virgata*, Hull, 25, p. 44.

The original description is as follows:—"Sub-circular, smooth, claret brown. Dorsal shield divided by a very shallow median furrow forked behind the middle and curved backwards on each side to the margin, leaving a transverse part behind which bears a pair of clavo-pectinate setæ. Two similar setæ stand in a line with these on the lateral margin. Epigyne oval, rounded at both ends, apiculate in front. Ventral shield reticulate."

This species should certainly be referred to the genus *Phaulocylliba*, Berlese. Apart from other differences it may be easily known from *Cylliba* by the absence of the marginal plates, a feature not referred to in the original description. The epigastric region of the venter is rather indistinctly defined and includes the anal foramen, so that the original figure (25, pl. 1. fig. 4) is inaccurate in this respect. The Irish specimens measure  $970\ \mu$  in length.

*Locality.* A few specimens found at roots of decayed Henbane plants at Clontarf, Co. Dublin, in August.

TRACHYUROPODA (DINYCURA) CORDIERI, Berl.

1916. Berlese, 11, p. 145.

A species referred by Dr. Berlese to the subgenus *Dinycura*, of which it is apparently the type. A characteristic feature is the double row of small piligerous plates lying between the extremities of the marginal shields at the end of the body, much as in the genus *Discopoma* except that there is but one row in this genus. These small plates vary greatly in number (16 to 22) in *T. cordieri* due to a few of them fusing with one another, or with the extremity of the marginal shields. The ventral line is thickly chitinized and divides the epigastric region into two parts, which lie at different planes. The female resembles the male in general structure; the epigyne is large and of the usual arch-like form, its ventral surface is strongly punctured and is produced anteriorly in a long chitinous process which ends in two or three points. Length of female  $563\ \mu$ , breadth  $357\ \mu$ . Identification verified by Dr. Berlese.

The *nympha heteromorpha* measures nearly  $550\ \mu$  by  $385\ \mu$ ; on the ventral side the area surrounding the acetabula is distinctly reticulate. The ventro-anal plate is of moderate size (length  $70\ \mu$ , breadth  $165\ \mu$ ); it is supported by a thick transverse bar which also forms the metapodial line.

*Locality.* The male, female, and nymph were not uncommon under damp wood lying on the Malahide sandhills, Co. Dublin, in September.

TRACHYUROPODA TROGULOIDES, Can. et Fan:ago, var. CELTICA, Halbt.  
(Pl. 21. fig. 18.)

1907. *Trachyuropoda celtica*, Halbert, 22, p. 67.

Described as a new species in the above reference, but more accurately placed as a variety of the present species, a decision in which Dr. Berlese agrees (*in lit.*). This variety differs from the typical form as described and figured by Italian acarologists (1, 5, 21) in its smaller size (length of female  $820\ \mu$ , breadth  $486\ \mu$ ; length of male  $742\ \mu$ , breadth  $436\ \mu$ ). The form is more parallel-sided, and the raised central part of the dorsum is of more uniform breadth throughout, while in the typical form its terminal part is much wider than the rest. The sculpturing of the ventral surface is also somewhat different (figured in 22).

*Localities.* Both sexes occurred in nests of the ant *Lasius niger* under stones at Tallaght, Co. Dublin, and it was also found in company with *Lasius flavus* on Lambay Island off the coast of Dublin. Mr. A. D. Michael found it with ants at Land's End, Cornwall (33), and Mr. H. St. J. K. Donisthorpe records it from other English localities associated with *Lasius niger* and *T. caespitum* (Entomologist's Record, 1909 and 1920).

*CILLIBANO DINYCHOIDES, Hull.*

1918. Hull, 25, p. 45.

A male *Cillibano* found in company with *Phaulorylliba virgata* (Hull) is probably to be referred to the present species. The Irish specimen agrees with the description except in the measurements (length about 717  $\mu$ ). The length of the English specimen is given as 655  $\mu$ .

The short description is as follows:—"Sub-circular, smooth, shining reddish brown, uniformly convex. Leg grooves exceedingly faint. Male genital aperture between coxæ iv. rather large (width 85  $\mu$ ). Femur ii. with a stout conical acute spine underneath. A clavate seta on each side of the anus, projecting beyond the posterior margin."

As is usual in this genus the marginal plates are entire, and in the present species they are separated from the dorsal plate by a very thin line running parallel to the margin in the posterior two-thirds of the body. The metapodial line curves inwards from the body margins to a point a little behind the insertions of the last pair of legs, and it is widely interrupted in the middle line of the body. The female is unknown.

*Locality.* One male found at roots of decayed Henbane at Clontarf, Co. Dublin, August.

*LABIDOSTOMMA LUTEUM, Kramer.*

The species recorded in the Clare Island Survey Report (23) as *L. cornuta*, Can. et Fanzago, is in reality *L. luteum*, Kramer. The former is a much larger species and differs also in certain details of structure; it has not been found in Ireland.

*L. luteum* is probably not uncommon in suitable localities in this country; in the Achill and Westport districts of Mayo it occurs under bark and amongst mosses growing on trees. In the Dublin and Wicklow district I have found it in pine woods.

*PHYLLOTEGEUS PALMICINCTUM (Michael).*

1888, *Leiosoma palmicinctum*, Michael, 32, p. 280.—1898, *Liacarus palmicinctum*, Michael, 34, p. 42.—1913, Berlese, 3, p. 92.

*Locality.* Apparently a rare species in Ireland, two specimens were found under stones at Doo Lough, near Muckross, Co. Kerry, in May. It is recorded by Michael as occurring on the lichen *Peltigera* at Land's End, Cornwall; so far as I can ascertain this Acarid has been found only in Britain.

*CARABODES AFFINIS*, Berl.

1913. Berlese, 8, p. 72.

Closely allied to *C. marginatus*, Michael, but may be known by the clavate abdominal hairs. Dr. Berlese assures me the Irish specimens are referable to this species, which he records as occurring under bark at Florence. The pseudostigmatic organ has a curved upturned stem and a somewhat flattened club. The lamellæ are broad, flat and granulate, and there appears to be a slightly raised ridge in the middle line of the cephalothorax. Interlamellar hairs stout and plumose at their extremities. The hairs of the dorsum as well as the marginal hairs are clavate, and their extremities are distinctly plumose.

*Locality.* Common amongst moss and lichens on the Portmarnock sandhills, Co. Dublin, in January. The *Carabodes* recorded as *C. marginatus*, Michael in (39) is the present species.

*ORIBATULA (HEMILEIUS) PLANTIVAGA*, Berl.

1892. *Oribatula tibialis*, Berlese, 1, Fasc. lxiv. n. 1.—1895. *Oribatula plantivaga*, Berlese, 1, Fasc. lxxvii n. 5 (reference in footnote).—1916. Berlese, 12, p. 322 (Redescribed).

*Localities.* Found near Mulranny, Co. Mayo, in September, and at Lucan near Dublin in company with *O. oblonga* and other species in February. Hull records it as occurring on rock lichens, *Physcia*, on the coast at Whitley Bay.

*DAMEOSOMA MACULOSA*, Warburton and Pearce. (Pl. 21. fig. 20.)

1905. Warburton and Pearce, 49, p. 567.

A *Dameosoma* found under bark in the Tolka Valley near Dublin (January) is apparently referable to this species. As it seemed not quite typical I sent drawings to Mr. Warburton, who has kindly verified the identification. The species is remarkable for the long, pointed cephalothorax, also the long lamellæ and the spotted dorsum, though, as the describers remark, these spots are in the epiostracum and are very easily rubbed off. This is so in the Irish specimen, in which they remain only near the margins. The pseudostigmatic organs are bent backwards, and carry on the anterior surface at least four distinct branches (Pl. 21. fig. 19 b); anterior margin of abdomen truncated. Length 418  $\mu$ .

*DAMEOSOMA MINUS*, Paoli, var. *LAMELLATA*, nov. (Pl. 21. figs. 19 a, b.)

1908. Paoli, 39, p. 48.

The form briefly described here must, I think, be identified as a variety of the present species. It differs from the type in the larger size and in the presence of well-defined lamellæ on the cephalothorax; in *D. minus* these are rudimentary.

Cephalothorax rather long and with sharply pointed extremity; lamellæ present in the form of two strongly curved ridges reaching from beyond the

middle to the pseudostigmata. The latter are circular and strongly chitinized. Sensory organs with a stout slightly curved stem and a large club-shaped extremity which is minutely spiculate. Abdomen elongate, pointed at both extremities, hairs very weak. Epimera well defined. Legs normal, monodactyle. Length  $240\ \mu$ , breadth  $110\ \mu$ .

*Locality.* Found under dead wood at Poulanass, Glendalough, Co. Wicklow, in March. The typical form is widely distributed, occurring in Italy and near Washington, U.S.A. (40).

*CYMBÆREMÆUS MONILIPES* (Michael).

1888. *Notaspis monilipes*, Michael, 32, p. 381.—1896. Berlese, 1, Cryptostig. ii. p. 37.

*Locality.* Glendalough, Co. Wicklow, in decayed tree-trunks, March.

*HERMANNIELLA GRANULATA* (Nicolet).

1855. *Hermannia granulata*, Nicolet, 35, p. 409.

In his well-known work on French Oribatids, Nicolet described and figured two species of *Hermannia*, i. e., *H. granulata* and *H. arrecta* (which he believed were distinct), differing from each other in the form of the cephalothorax. As far as I am aware the distinctness or otherwise of these species has not been settled. It seems likely, however, that Nicolet's specimens, which were found in the same localities, represent but a single species, and that the supposed differences in the form of the cephalothorax may be more apparent than real. There is a tendency among acarologists to record *H. granulata* in preference to *H. arrecta*, it is also the first mentioned of the two species in Nicolet's monograph, so I think it is better to refer the Irish specimens here until the question has been decided.

*Localities.* Adults and nymphs were found in some numbers in a decayed birch log at Glendalough in April, and it has also occurred in moss collected at Howth, Co. Dublin, in June.

*TARSONEMUS LATICEPS*, sp. nov. (Pl. 21. figs. 21 a-c.)

A species allied to *T. culmicolus*, which is recorded by Reuter (41) as causing injury to meadow grasses in Finland. Differs in the form of the body, the broader capitulum, and in other details.

*Female.* Form rather short and broad (length  $195\ \mu$ – $210\ \mu$ , breadth  $110\ \mu$ ); in ovigerous females the body is more elongate, becoming long oval (length  $215\ \mu$ ), the enclosed egg measuring about  $115\ \mu$ . Side margins sub-parallel, front margin truncated and half covering the head, end margin rounded. Division between the cephalothorax and abdomen and the one at the middle of the latter distinct, but the segments at end of the abdomen are ill-defined. Hair armature very short except for the usual long pair close to the sides of the cephalothorax, and a shorter pair at the angles of the front margin. The sensory organs (Pl. 21. fig. 21 a) arising from small circular stigmata, are large, they may be either globular, or leaf-like with pointed extremities, and both



forms may be present in the same individual. The capitulum is very large and wide in relation to the length (breadth about  $40\mu$ ), truncated in front and obtusely round at the end margin. Epimera of the first pair of legs strongly defined. The first two pairs of legs are short and stout; the long terminal hair of the end pair is strongly recurved.

*Male* (Pl. 21. fig. 21 *b*). Form of the main body much as in female (length  $180\mu$ – $215\mu$ , breadth  $85\mu$ – $100\mu$ ). The capitulum is less transverse (breadth  $35\mu$ ), and the hair armature is stronger, there are two pairs of long hairs on the cephalothorax. Legs short and stout; fourth pair (Pl. 21. fig. 21 *c*) shaped much as in *T. floricolus*, being without blades; second segment straight, inner margin slightly sinuate at the extremity; two hairs are present. Third segment armed with a long spine-like hair, and at the base is another shorter hair. As in *T. brevipes* the front margins of the third and fourth epimera are ill-defined.

The male larva is as long as the adult (length  $215\mu$ ), due to the large size of the post-abdominal part. Epidermis distinctly striated. Legs stout and of very uniform size. The terminal part of the abdomen is strongly constricted and is narrower (breadth about  $50\mu$ ) than the main body, and there are two stout outwardly curved hairs at the apex.

The eggs of this species are large (length  $125\mu$ – $135\mu$ , breadth  $65\mu$ ), they are of a regular long oval form and the surface is marked with numerous light-refracting punctures.

*Locality.* Found in numbers in partly decayed Narcissus bulbs in County Dublin, January. The place of origin of the bulbs is uncertain.

At least three other species of *Tarsonemus* have been found in Ireland. One of these, noticed injuring oats at Killyarden, Co. Donegal, in August last, is possibly referable to *T. spirifer*, Marchal, the female agreeing well with Korff's figure of this species which is reproduced by Soraue (Handbuch der Pflanzen-Krankheiten, iii. p. 102). The male of *T. spirifer* has the fourth pair of legs peculiarly modified, and until this sex is found this identification must remain somewhat doubtful.

The form of this female is a regular long oval (length  $235\mu$ , breadth  $110\mu$ ). The capitulum is rather broad (breadth  $35\mu$ ), but less so than in *T. laticeps*. The sensory organs are very distinctly leaf-shaped with sharply pointed extremities. The first two pairs of legs are short and stout.

This species was communicated by Dr. G. H. Pethybridge, who tells me it attacks oats in much the same way as *T. culmicolus*, Reuter, attacks meadow grasses in Finland. Reuter says the mites are found on the haulm, presumably within the leaf-sheath within the first node; they suck out the juices so that the inflorescence wilts and dies.

Females of *T. floricolus* were found on gooseberry plants at Lisburn, Co. Antrim, in July.

Colonel Samman tells me he finds *Acarapis woodi*, Hirst, commonly in the tracheae of Irish honey-bees.

**BIMICHAELIA CRASSIPALPIS**, sp. nov. (Pl. 21. figs. 22 *a*, *b*.)

Allied to *B. setigera*, Berlese (4, p. 13), but larger, the palps are stouter, the shoulders less prominent, and the structure of the skin, which is elaborately sculptured, is different.

Colour white. Form sub-pentagonal (Pl. 21. fig. 22 *a*), shoulders prominent but less so than in *B. setigera*. Epidermis striated and marked with a distinct hexagonal pattern, the hexagons forming rosette groups round the body hairs, the latter are sparse and are branched at the base (fig. 22 *b*). Cephalothorax not well marked off from the abdomen; a narrow area enclosed by chitinous rods lies in the middle line, and two long sensory hairs are placed at its proximal extremity; behind these hairs are two semicircular stigmata. I can find no trace, however, of the small, clubbed, sensory organs which arise from these in other species of the genus (in a second specimen from another locality they are also absent); it is likely, however, that such organs may be sometimes present in the species. Abdomen thrown into folds and constricted at the middle, apex somewhat truncate. Palps stout. Legs short and very robust, distinctly areolated, hairs similar to those of the body. Length 320  $\mu$ , breadth 240  $\mu$ .

*Localities.* Found in sphagnum moss collected by Mr. A. W. Stelfox on the Garron Plateau, Co. Antrim, in July. It has also occurred in damp moss from Glencullen, Co. Dublin, in April of the present year.

**ALICUS ROSTRATUS**, Träg.

An *Alicus* found in two highland localities in Ireland agrees excellently with the present species, which is recorded from the Sarekgebirge (Swedish Lappland), except that the rostrum seems shorter than is described and figured (46). Drawings were sent to Dr. Trägårdh, and he believes there is a difference in this respect. However, they agree in so many characters that it does not seem desirable to describe the Irish specimens under a new name.

The colour during life is a reddish purple. Length 460  $\mu$ , breadth 270  $\mu$ . Cephalothorax with a distinct rostrum, and well marked off from the abdomen, central area defined by two subcutaneous chitinous ridges, the hinder part of which is areolated at the middle, and encloses the usual two pairs of long sensory hairs. Eyes small but distinct, placed on the front of lateral swellings. Abdomen with moderately marked shoulders and a sparse covering of short, spiculate hairs; during life the dorsum lies in distinct folds. Legs longer and more slender than is usual in this genus.

*Localities.* Found in moss collected on the Comeragh Mountains, Co. Waterford, in July; and in sphagnum from Glendhu, Co. Dublin, in October.

**SOIRUS INERMIS**, Träg. (Pl. 21. figs. 23 *a*, *b*.)

This species was described from specimens found on the surface of a small reservoir (Wassersammlung) at Gizeh, Cairo, in December 1900 (45). There can scarcely be any doubt that the specimens here recorded are the

same species. The palpi, which are characteristic in the species of this genus, are identical with those of *S. inermis*, Träg. Dr. Trägårdh, to whom drawings were sent, agrees with me in this identification. The following is a brief description of the Irish form:—Colour red (length  $490\mu$ ). Body of the usual subrhomboidal form, shoulders prominent, the body margins gradually narrowing to the posterior margin where there are three small lobes. Epidermis minutely lined. Maxillary plate longer than broad; mandible long (length about  $286\mu$ ), extremities reaching to near the end of the second palp segment. Palps (Pl. 21. fig. 23 b) long and slender, apparently four-segmented, second and third segments armed at their ventral extremity with a strong spatulate hair. Legs long and of very uniform thickness so that the tarsi are truncated at the ends, where they are armed with two flat lobes and small claws. Length of the first pair  $510\mu$ , of the fourth  $530\mu$ .

*Locality.* Found amongst dripping wet moss and liverworts (*Conocephalus conicus*) at the overflow of a small reservoir at Greystones, Co. Wicklow, July 1920, with such species as *Notaspis lacustris*, *Oribata lucasi*, *Episeius italicus*, and others.

*NEOPHYLLOBIUS SAVAILLIS*, sp. nov. Pl. 21. figs. 24 a, b.)

Colour as in *N. elegans*, Berl. Form oval, cephalothorax not well marked off from abdomen. Eyes double lensed. There is a double row of six strong hairs, placed rather close together, down the middle of the body, and a row of eight similar hairs along each outer margin; all of these hairs are spiculate, rather strongly curved and arise from small tubercles. Epimera large, inner margins indistinct, with from two to three hairs which are much weaker than those of the dorsum. Genital area tapering to a point and enclosing a small anal plate with four marginal hairs. Rostrum triangular, ending in a single lobe. Palps very short and stout, second segment longer than the two end segments together, with two dorsal spines, one spiculate and stronger than the other; third segment with one dorsal spine; fourth segment ending in two curved spines, and carrying an appendage which is contracted at the apex and has three spines.

Legs much as in *N. elegans*, Berlese; there is a long spiculate hair on the third segment of each leg, that of the last pair bent at the end, length about  $264\mu$  (fig. 24 b). The legs measure about  $396\mu$ ,  $330\mu$ ,  $363\mu$ , and  $420\mu$  in length.

A species allied to *N. elegans*, Berlese (1, Fasc. xxxiv. n. 5), but differing in the size and form of the body. The median dorsal series of spines are more numerous and are placed closer together, and the long hairs on the third segment of the last pair of legs are shorter and of different form. Verified by Dr. Berlese.

*Locality.* Not uncommon on lichen-covered rocks at Howth summit, Co. Dublin, September.

**BRYOBIA HUMERALIS**, sp. nov. (Pl. 21. figs. 25 a-c.)

A small species, length about 330  $\mu$ , breadth 270  $\mu$ . Colour red. Body strongly and suddenly narrowed at both extremities, shoulders very prominent. Frontal tubercles of cephalothorax comparatively short, carrying strongly-curved spatulate hairs (Pl. 21. fig. 25 b). End margin of abdomen with five pairs of similar hairs, the three inner pairs being very conspicuous; there is also a double row of three or four hairs near the middle line of the body and a pair at the shoulders. Palps very short, appendage of fourth segment large and stout, terminal claw strongly curved. Legs shorter and stouter than in *B. pretiosa* and of more uniform breadth, the second segment of the first pair being noticeably shorter; the two end segments are of nearly equal length (Pl. 21. fig. 25 c).

Apart from the difference in the legs, this species may be known from *B. pretiosa* by the smaller size, the shorter frontal tubercles, the more strongly narrowed body, the more prominent shoulders, and the longer body hairs.

*Localities.* Found at Clontarf, near Dublin, in March 1907. The correspondent who sent me the specimens had his attention drawn to them by the patches of red colour on a garden wall caused by the presence of large numbers of this mite. North shore of Lough Neagh, in wet moss, August 1922. Mr. Evans has found the species amongst moss collected near Edinburgh.

**RHAPHIGNATHUS PATRIUS**, Berl., var. **TRUNCATUS**, nov. (Pl. 22. figs. 26 a-c.)

A robust form evidently allied to *R. patrius*, Berl., and in all probability a variety of this species. Differs notably in the narrower body; of the type Dr. Berlese remarks: "fere æque longium ac latum humeratum"; the end margin is very distinctly truncated, and the areolations of the epidermis are fewer and larger.

Length 420  $\mu$ , breadth 320  $\mu$ . Colour blood-red, with a central dark area in front and four dark blotches on each side of the body, much as in Berlese's drawing of *B. clavatus* (1, Fasc. xxii. n. 2). Cephalothorax bluntly pointed in front, the sides slightly sinuate behind this, and they merge evenly with the shoulders of the abdomen; the margins of the latter narrow gradually to the truncated end margin, at each angle of which there is a hair somewhat longer than the body hairs. There are nine pairs of hairs in all, including the frontal hairs, and the latter are the only ones which have a trace of secondary hairs. Epidermis very coarsely punctured, and there are paired circular pits close to the shoulders; the end of the dorsum is slightly depressed. On the ventral side the anal plate and the areas surrounding the epimera are strongly areolated, and on the hinder margins of the former are two spine-like hairs. Palps (Pl. 22. fig. 26 b) very stout; second segment with a long, bent hair, which may, apparently, be either simple or trifid at the extremity; third segment with a similar dorsal hair; length of palp about

95  $\mu$ . Legs very stout (length of first pair 264  $\mu$ , of fourth pair 254  $\mu$ ), with strong dorsal hairs, which are spiculate at the base (Pl. 22. fig. 26 c).

*Locality.* A single specimen found amongst wet moss from the banks of a mountain-stream at Glencullen, Co. Dublin. Collected by A. W. Stelfox in October 1921.

I have also found amongst moss in a mountain-stream at Kilmashogue, Co. Dublin, a *Rhaphignathus* the identity of which is uncertain. It is very closely allied to a form described by Trägårdh as *R. patrius* var. *brevipalpis* (46, p. 470). The Irish specimen differs in the smaller size (length 368  $\mu$ , breadth 275  $\mu$ ); it is less rotund, the puncture less regular, and the palps are relatively larger.

*RHAPHIGNATHUS PLUMIFER*, sp. nov. (Pl. 22. figs. 27 a, b.)

A very distinct species, which may be easily known from its congeners by the small size, the strongly plumose hairs, and the beautiful sculpturing of the epidermis. Verified by Dr. Berlese.

*Male.* Length 210  $\mu$ , breadth 120  $\mu$ . Colour bright red. In shape resembling *R. sirulus*, being ovate, though the end of the body is produced in a point. All of the body hairs are strongly plumose. The epidermis is marked with a very distinct polygonal pattern as well as being punctured (fig. 27 b). Cephalothorax large in relation to the abdomen, carrying three pairs of hairs and a strongly-curved pair of frontal hairs. Eyes small yet distinct, and placed on the side margins. The main abdomen is much higher than the apical part, and is truncated at the end, where there are two rather long (40  $\mu$ ) hairs, curved inwards at the extremities. In addition to these there are six pairs of hairs on the dorsum. Epimera well defined; anal plate large, rounded on the front margin. Maxillary plate transverse; rostrum sharply pointed. The palps are very stout, second segment with two strongly-plumose hairs. Legs short and robust, armed with both simple and plumose hairs like those of the body.

*Locality.* A single specimen found under a stone amongst heather on Howth Head, Co. Dublin, in September.

*RHAPHIGNATHUS LONGIPILIS*, sp. nov. (Pl. 22. fig. 38.)

Colour blood-red with blackish markings. Form short and broad. Front margin obtusely pointed, end margin rather truncated. Eyes small, placed near middle of side margins. Upper surface of cephalothorax and abdomen with a distinct, raised polygonal network. Abdomen well defined, shoulders rather prominent. Hair armature, including the frontal bristles, very long (about 125  $\mu$ ), curved towards their extremities, and there is no trace of secondary hairs. Epimera small. Maxillary plate transverse. Palps very short and robust, distinctly stouter than the legs. The latter are of moderate length, and rather slender for this genus. Length 290  $\mu$ , breadth 380  $\mu$ .

*Localities.* Found amongst damp moss at Glencullen in April, and in moss collected from pools in the River Dodder, at Old Bawn, in May, by Mr. A. W. Stelfox. Both localities are in Co. Dublin.

*STIGMÆUS ANTHRODES*, Berl., var. *RETICULATUS*, nov. (Pl. 22. figs. 28 a, b.)

A large, robust species. The Irish specimens are to be referred to a variety in which all of the body plates are sculptured with a very distinct, polygonal reticulation. Colour bright red. Cephalothorax protected by a large central shield and two small plates at the posterior corners. On the dorsum of the abdomen are ten shields, comprising three on the anterior part, then four smaller ones in a transverse row; behind these are two similar plates, and a large unpaired shield lies at the end of the abdomen. The palps, legs, epimera, and ventral plates are all marked with a polygonal network. Length 550  $\mu$ , breadth 310  $\mu$ .

*Localities.* Amongst hay brought into a cave at Doneraile, Co. Cork, in July. Under refuse on the sea-bank at Malahide, in May. Amongst garden refuse at Rathgar, Dublin, in April. Mr. A. W. Stelfox found it abundantly in the last-mentioned locality.

*CALIGONUS SCAPULARIS* (Koch), Berlese.

A shining red species of very convex form. The eyes are very large and the body hairs are long and curved.

*Localities.* In sphagnum, Lough Dan, in August, and in moss from pools by the River Dodder, near Tallaght, in May.

*CHEYLETUS VENUSTISSIMUS*, Koch.

*Locality.* Found in numbers on a Hay Moth (*Caradrina*) at Sandymount in November by Mr. J. G. Rhynchart. *Cheyletus eruditus*, Schr., has been found on pine-shoots in August.

### HYDEACARINA.

*Drammenia crassipalpis*, Sig Thor. The genus *Drammenia* was established by Thor in 1913 (44) with *D. elongata* as the type-species. In the same paper Thor partially described a second species, *D. crassipalpis*, but apparently the single specimen, found at Drammen in Norway, was lost before a description had been made; such characters as are mentioned chiefly refer to points in which this species differs from *D. elongata*. As far as one can judge from these notes, the form briefly described below is in all probability the same as *D. crassipalpis*, Thor. Colour yellow with brown coecal markings. Length 474  $\mu$ , breadth 374  $\mu$ . Cuticle strongly chitinized, except for a marginal band separating the dorsal and ventral plates. Front margin truncated, sides gradually increasing in width to beyond the middle of the body, posterior margin slightly flattened. Dorsal plate punctured, touching

the front margin of the body, separated from edge of ventral plate at the side and end margins by a rather broad band of soft, striated cuticle, which contains about five pairs of pores. On the dorsal plate is a double row of similar pores, near each of which is a fine hair. Eyes placed at each corner of the front margin on the dorsal outline of the body. Frontal bristles very short (Pl. 22. fig. 29 a). Epimeral region much as in *D. elongata*, except the outer border of the fourth pair, instead of being absent, is indistinctly defined (Pl. 22. fig. 29 b). The genital plate is shorter (length 132  $\mu$ , breadth 100  $\mu$ ). Length of maxillary plate to tip of rostrum 120  $\mu$ . Palps very stout, the second segment broader than the legs (breadth in dorsal view 49  $\mu$ ); on its inner ventral margin is a low, rounded prominence and a strong hair as in the type-species. Inner distal angle of the fourth segment produced in the form of a strong triangular tooth, and beside this is a smaller tooth, both bearing fine hairs; near the dorsal line of the palps are a few short spines (Pl. 22. fig. 29 c). Legs of moderate length, stout, armed with short spines and without swimming-hairs; the lengths are about 240  $\mu$ , 374  $\mu$ , 330  $\mu$ , and 410  $\mu$ .

*Locality.* A single specimen found amongst sphagnum moss collected on Ott Mountain, in the Mourne Mountains, in May by Mrs. R. F. Scharff.

*Ljanja bipapillata*, Sig Thor, has been found in the River Dodder, near Dublin, in November; in the River Dorgle, at Powerscourt, and in the stream flowing between the lakes at Glendalough, Co. Wicklow, in April. The colour of living specimens is pale yellow with brownish markings. *Megapus gibberipalpis*, Piersig (40), occurs in streams on the Dublin Mountains at Kilkee and Kilmashogue, and in the River Liffey. Also in the stream flowing from Lough Bight, on Carruntuohill Mountain, in Co. Kerry. *Arrhenurus insulatus*, Koenike: a single immature specimen of this species occurred in a small Chara pool at Gollierstown, Co. Dublin, in October. The male has not been described. The female is red in colour, and is remarkable on account of the large wing-shaped genital plates and the long and narrow epimera especially of the third and fourth pairs. The species is well figured by Dr. Koenike (26); the type was found on Norderney. I believe this species has also been found by Mr. C. D. Soar in England.

Apart from a few records of the common *Hydryphantes ruber*, de Geer, nothing has been published on the species of *Hydryphantes* occurring in Ireland. I have recently been making a preliminary examination of specimens of this interesting genus from various Irish localities, and find there are at least six species found in this country, counting *H. prolongatus*, Thon, of specific rank. A certain amount of variation occurs in the form of the eye-plates of *Hydryphantes*; and as the structure of the plates is of great use in the identification of the species, a series of figures are given in the present paper, in the hope that they may be of interest for comparison with those of the same species in other countries.

The type-species of the genus, *H. ruber*, de Geer, is common and widespread in Ireland (Pl. 22. fig. 30), as is also *H. prolongatus*, Thon (Pl. 22. fig. 31), which is sometimes recorded as a variety of the former; in my experience it is rather the exception to find both of these occurring in the one locality. The first-mentioned has been found in ponds and lakes in Donegal, Antrim (L. Neagh), Monaghan, Galway, Wexford and Dublin, and the latter in Donegal, Dublin, Kildare, Galway and Kerry. *H. prolongatus* is perhaps of more frequent occurrence. The eye-plate and palps of a curious form, which must, I think, be regarded as an aberration of *H. prolongatus*, are figured (Pl. 22. figs. 32 *a*, *b*). The general structure is as in the species, but the eye-plate is smaller and narrower especially across the front margin (length along middle line  $363\mu$ , breadth  $373\mu$ ), and the median eye is placed much nearer the middle of the plate. Unfortunately, only one specimen was found in a small lake on Lough Salt Mountain, in Donegal. *H. bayeri*, Pisarovic (Pl. 22. fig. 33), is apparently rare; I have found a single specimen in a drain by the River Shannon, at Portumna, in June. *H. bayeri nonundulata*, Viets (Pl. 22. fig. 34) was found in a pool at the entrance to Glenshelane Valley, at Cappoquin, Co. Waterford, in June. It has also occurred under stones on the marshy edge of Bount Brown Lough, near Westport, in Co. Mayo. The water-level of the lough had fallen considerably at the time (July 1911). In the structure of the eye-plate this form bears a strong resemblance to *H. planus*, Thon, but the plate is more abruptly narrowed behind the anterior corners, the breadth across the hinder part is relatively greater, and the posterior emargination is less deep than in *H. planus*. The median eye is placed far back as in the type. Viets records this form from Eastern Prussia (47). *H. crassipalpis*, Koenike, was found in ponds near Enniscorthy, Co. Wexford, in May. This species may be easily recognized by the form of the eye-plate and the short, thick palps; described by Dr. Koenike from Borkum and the neighbourhood of Bremen, where it is rare (27). At Killarney I have found a *Hydryphantes* which seems referable to a form of this species. The eye-plate (Pl. 22. fig. 35 *a*) is smaller (length along middle line  $298\mu$ , breadth  $418\mu$ ) and the anterior corners are most acute; the sides are more deeply indented, and the posterior emargination is deeper. The palps (fig. 35 *b*) are shorter (length about  $300\mu$ ) than in the typical form; the second segment (length  $110\mu$ ) has four short dorsal spines on the upper surface and three longer, feathered hairs placed at the upper corner of the inner surface of the segment. This form, which may be called *lacustris*, forma nov., was found in Loosacaunagh Lough, between Killarney and Kenmare, in the month of April. *H. placationis*, Thon (Pl. 22. fig. 36), not common; found in ponds near Galway in June, and in ponds in the Phoenix Park, Dublin, in April. *H. dispar* (Schaub) is apparently rare in Ireland; found in company with the preceding species in ponds in the Phoenix Park in April. The eye-plate is figured (Pl. 22. fig. 37).



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## EXPLANATION OF THE PLATES.

### PLATE 20.

- Fig. 1. *Gamasus (Eugamasus) crussitarsis*, sp. nov. Male. a. Chelicerae. b. Second leg. c. Process on outer side of femur of second leg, dorso-ventral view.
2. *Gamaecellus (Protolaelaps) granulatus*, sp. nov. Female. a. Under side. b. Part of dorsal plate and soft epidermis.
3. *Gamaecellus (Protolaelaps) subnudus*?, Berl. Larva.
4. *Laelaps latisternus*, sp. nov. Female. Under side.
5. *Laelaps simplex*, sp. nov. Female. Under side.
6. *Laelaps funbriatus*, sp. nov. Female. Genital and ventro-anal plates.
7. *Lasioseius (Lasios.) gracilis*, sp. nov. Female. a. Upper side. b. Hair of posterior margin. c. Ambulacrum.
8. *Lasioseius (Lasios.) ometes*, Oudem. Female. a. Under side. b. Shoulder bristle. c. Chelicerae.
9. *Lasioseius (Epioseius) glaber*, Berl., var. *curtipes*, nov. Female. Under side.
10. *Lasioseius (Epioseius) sphagni*, sp. nov. Female.

- Fig. 11. *Lasioseius (Episeius) italicus*, Berl. Male chelicerae.  
 12. *Lasioseius (Episeius) michaeli*, sp. nov. Male chelicerae.  
 13. *Lasioseius (Episeius) major*, sp. nov. Female: a. Under side. Male: b. Chelicerae.  
 14. *Lasioseius (Platyseius) subglaber* (Oudem.). Male chelicerae.  
 (The male chelicerae figured in 11, 12, and 14 are drawn to the same magnification.)

## PLATE 21.

- Fig. 15. *Zercon tragardi*, sp. nov. a. Upper side. b. Plumose hair.  
 16. *Ceratozercon bicornis* (Can. et Fanzago). One of the terminal tubercles.  
 17. *Polyaspinus cylindricus*, Berl. Upper side.  
 18. *Trachyuropoda trogluoides*, Can. et Fanzago, var. *celtica*, Halbt. Upper side.  
 19. *Damaosoma minus*, Paoli, var. *lumellata*, nov. a. Upper side. b. Pseudostigmatic organ.  
 20. *Damaosoma maculosa*, Warburton and Pearce Cephalothorax.  
 21. *Tarsonemus laticeps*, sp. nov. Female: a. Anterior part of cephalothorax. Male: b. Under side; c. Fourth leg.  
 22. *Bimichaasia crassipalpis*, sp. nov. a. Upper side. b. Hexagonal marking of epidermis.  
 23. *Scirus inermis*, Trägårdh. a. Upper side. b. Palp.  
 24. *Neophyllobius saxatilis*, sp. nov. a. Upper side. b. End segments of the fourth leg.  
 25. *Bryobia humeralis*, sp. nov. a. Upper side. b. Body hair. c. First leg.

## PLATE 22.

- Fig. 26. *Rhaphignathus patrius*, Berl., var. *truncatus*, nov. a. Upper side. b. Right palp. c. Segment of leg.  
 27. *Rhaphignathus plumifer*, sp. nov. a. Upper side. b. Epidermis.  
 28. *Stigmaeus anthrodes* var. *reticulatus*, nov. a. Upper side. b. One of the dorsal shields.  
 29. *Drammenia crassipalpis*, Sig Thor. a. Upper side. b. Epimeral region. c. Palp.  
 30. *Hydryphantes ruber*, de Geér. Eye-plate (River Naun).  
 31. *Hydryphantes prolongatus*, Thon. Eye-plate (Galway).  
 32. *Hydryphantes prolongatus*, Thon (Ab.). a. Eye-plate. b. Palp (Donegal).  
 33. *Hydryphantes bayeri*, Thon. Eye-plate (River Shannon).  
 34. *Hydryphantes bayeri* var. *nonundulata*, Viets. Eye-plate.  
 35. *Hydryphantes crassipalpis*, Koen., forma *lacustris*, nov. a. Eye-plate. b. Palp.  
 36. *Hydryphantes placationis*, Thon. Eye-plate.  
 37. *Hydryphantes dispar*, von Schaub. Eye-plate.  
 38. *Rhaphignathus longipilis*, sp. nov. Palp.

(All eye-plates of *Hydryphantes* are drawn to the same magnification, with the exception of number 35.)

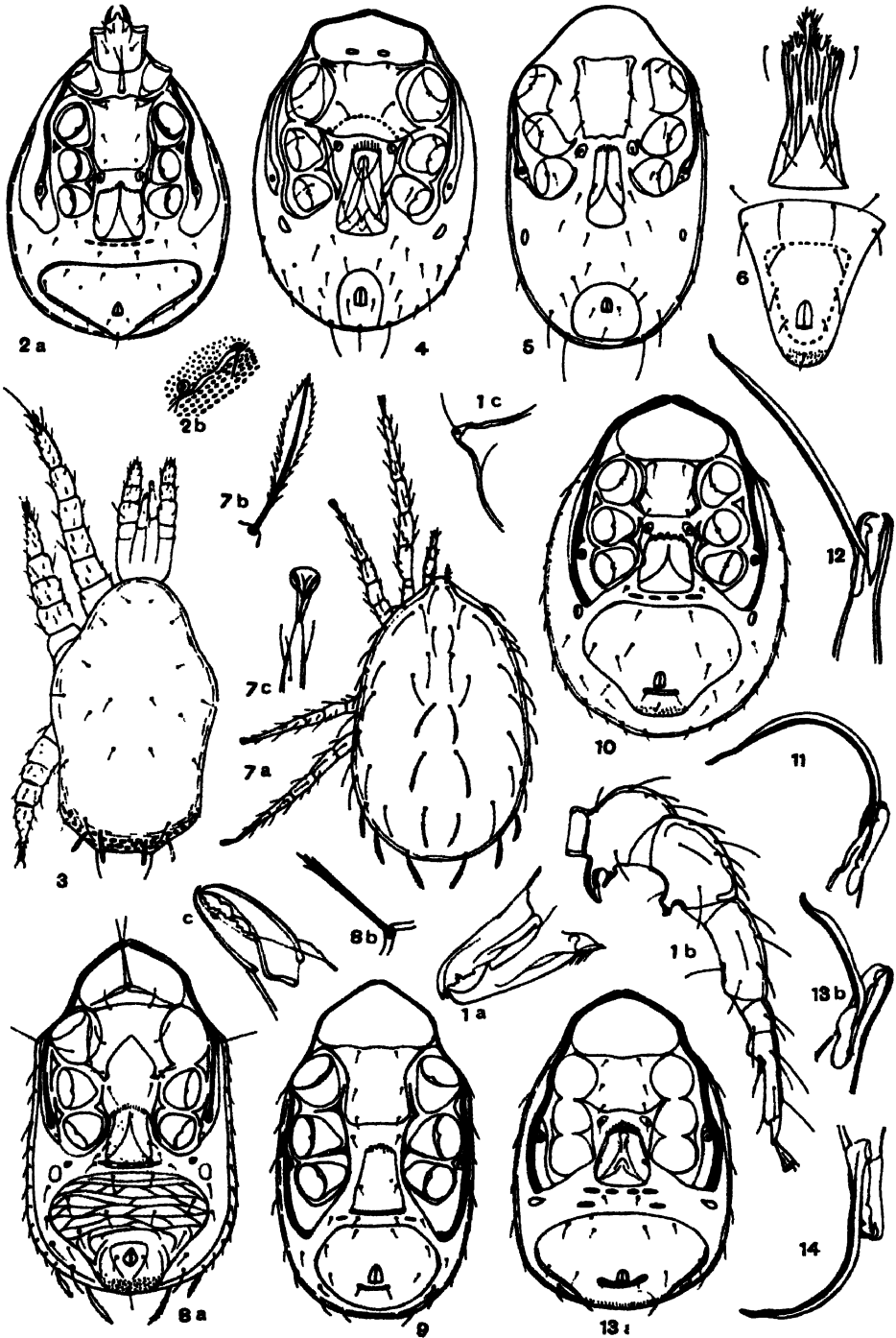
**Note I.**—*Lasioseius (Lasio.) ometus*, Oudem.

In a paper just received, Vitzthum describes and figures this species from Austrian specimens found in the borings of "bark-beetles." (Arch. f. Naturg. 89 Jahrg. 1923.)

**Note II.**—*Drammenia crassipalpis*, Sig Thor. Additional localities for this species are—Stream above Lough Nahanagan at 1500 feet, in submerged moss in June. Glencree, amongst wet moss and sphagnum at 500 feet in September; both of these localities are in the County Wicklow. Also amongst sphagnum on Featherbed Mountain in County Dublin at an elevation of 1600 feet, in September 1922.

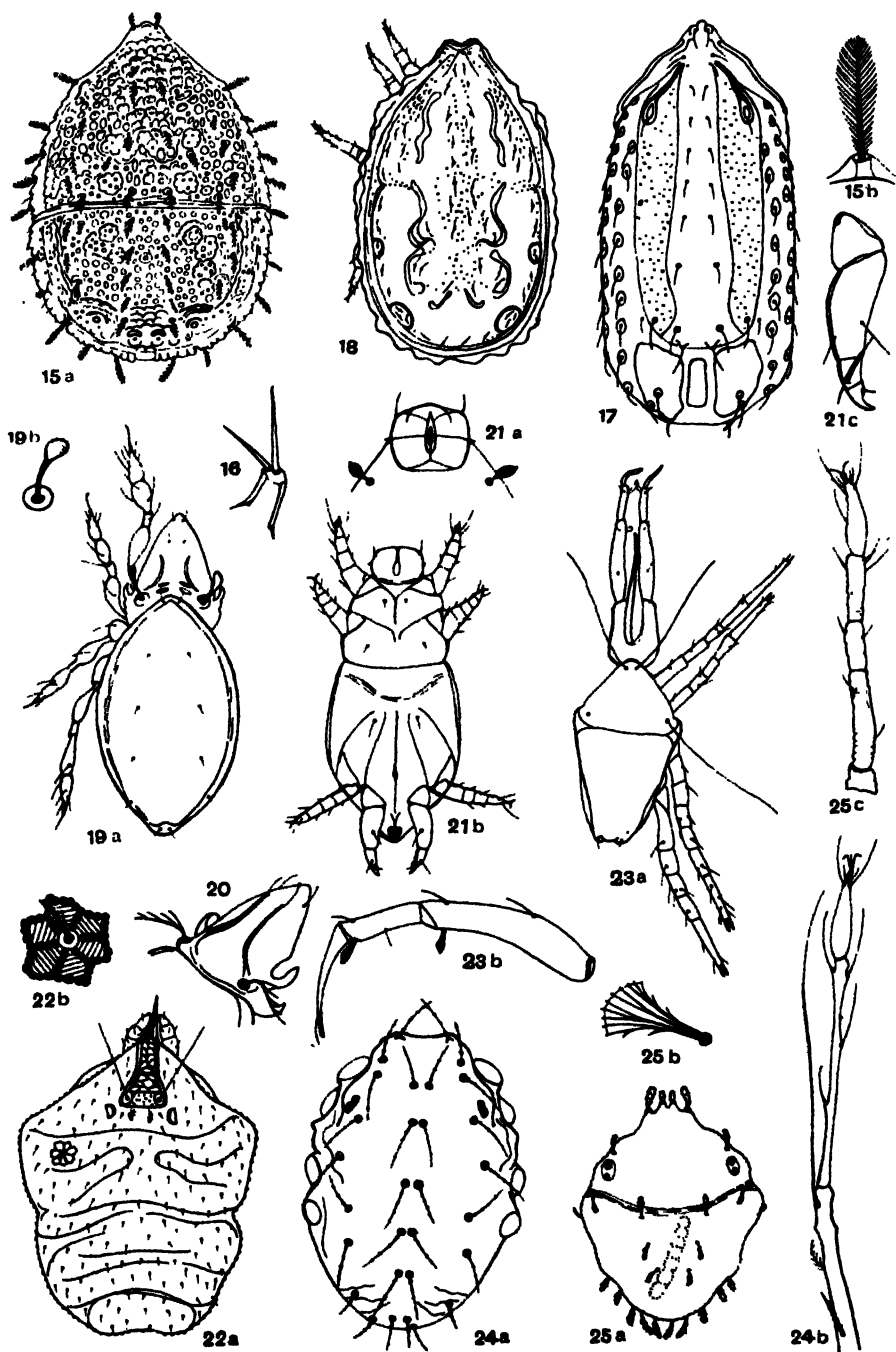
4th July, 1923.

J. N. H.



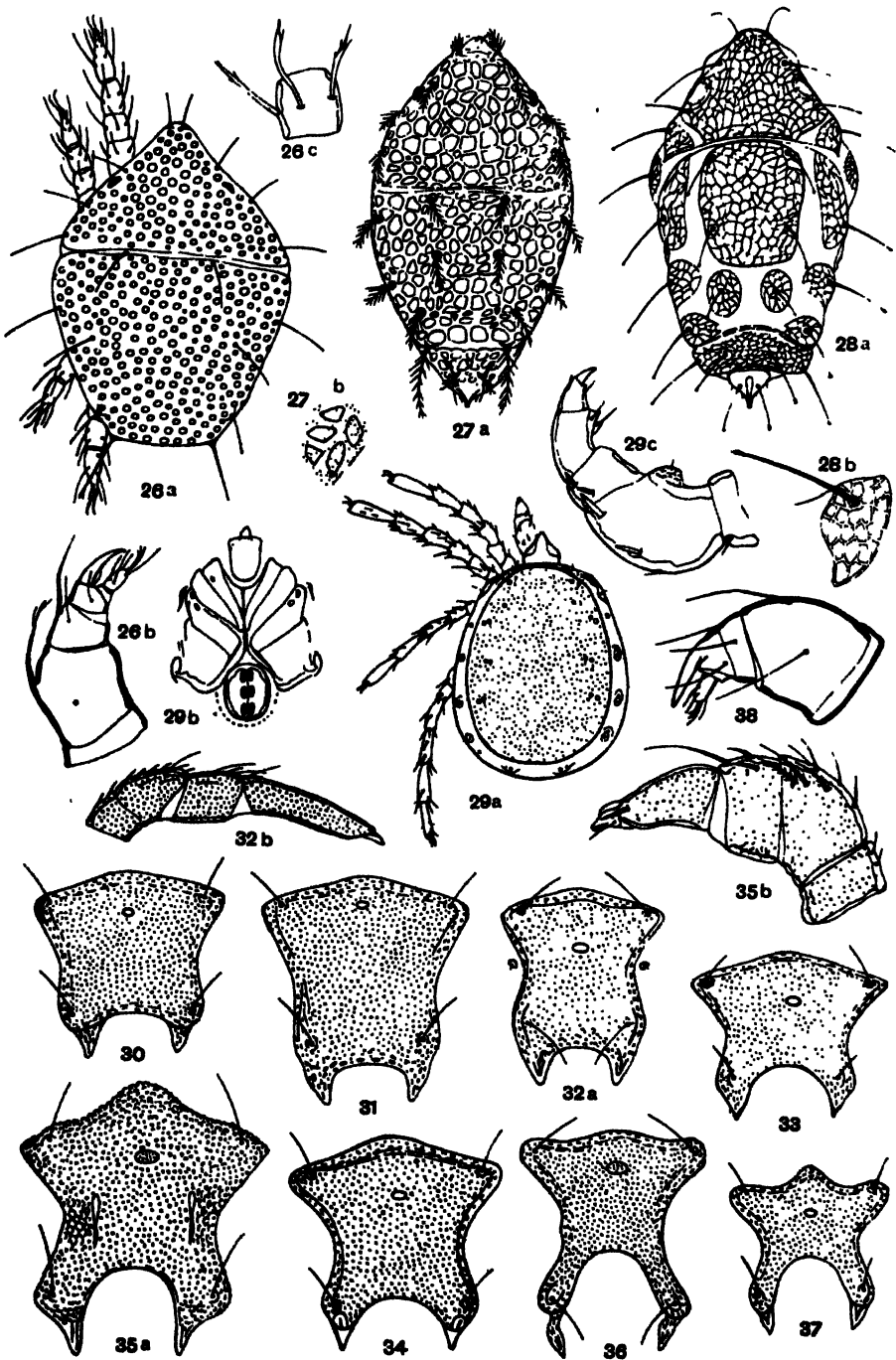
SPECIES OF ACARI.





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**Albion of Dimorphism and Asexual Reproduction in *Ptychodera capensis* (Hemichordata).** By J. D. F. GILCHRIST, M.A., D.Sc., F.L.S.,  
Professor of Zoology in the University of Cape Town

(With 7 Text-figures)

[Read 7th June, 1923]

THE Hemichordata, considered as including the three groups represented by *Cephalodiscus*, *Balanoglossus*, and *Phoronis*, are of such importance as possible connecting links between the great groups of Vertebrates and Invertebrates that any new facts bearing on their relationship to each other or to other phyla of the animal kingdom are of particular importance. The following observations on a species of *Balanoglossus*, which exhibits a form of dimorphism, associated with sexual and asexual reproduction, may therefore be of special interest.

There appear to be at least four different species of "*Balanoglossus*" in S. Africa: three, which I have already described (Trans. Phil. Soc. S. Afr.: vol. xvii. pt. 2, p. 151, 1908, and Ann. S. African Museum, vol. vi. pt. 2, p. 207, 1908), *Ptychodera capensis*, *P. polygerans*, *P. natalensis*, and an undescribed species, of which only a single imperfect specimen has as yet been found. The first and second were found in a tidal sandy pool in False Bay, the third in the muddy mangrove-bordered flats of Durban Bay, the fourth in a crevice of a rock at low-water mark in False Bay. The first two are obviously different from the third and from the fourth, which does not belong to the genus *Ptychodera*. The first two also seem to be quite distinct from each other, but their constant association in the same pool, their external resemblance in all but the posterior regions of the body, and the fact that they both undergo a normal process of asexual multiplication in one of them, all lead to the suspicion that they might represent sexual and asexual forms of the same species.

As far as I know, the genus *Ptychodera*, the *Tauroglossus* of Spengel, is distinguished by specific difference in size, shape, or structure of the body. The size, shape, colour, and position of the collar, the position of the collar, the size, shape, colour, and position of the collar are also similar. The differences in the posterior regions of the body are, however, well marked, for (1) in *P. capensis* there is no hepatic caeca, either external or internal, and the intestine is not clearly marked off from the branchial caeca, which seem to be continued into this caeca. In *P. polygerans* and *P. natalensis*, on the other hand, the intestine is never continued into the caeca, and asexual reproduction takes place by

successive fragmentations or proliferations at the extremity of the tail; (4) a further difference is that, though the two species were found in the same locality and under the same conditions, they do not usually occur at the same season, *P. capensis* being found chiefly, often exclusively, in the winter months, *P. proliferans* in the summer months, a fact which may, however, indicate a possible relation between the two species. To determine this point extensive collections were made at various seasons, but no indication of any

FIG. 1.

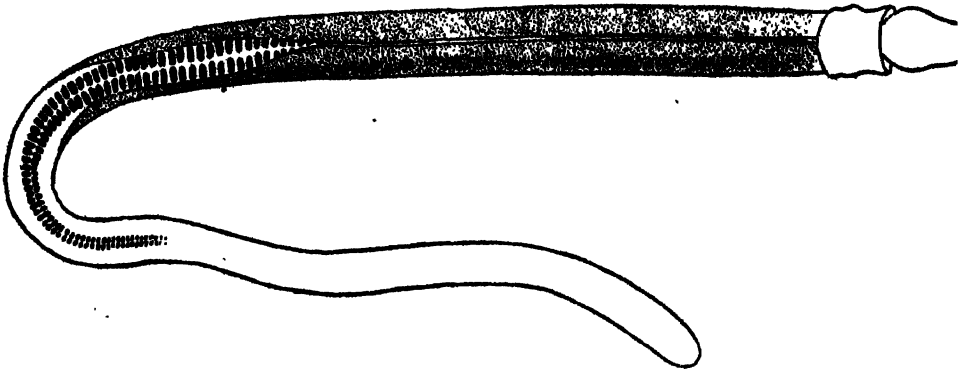
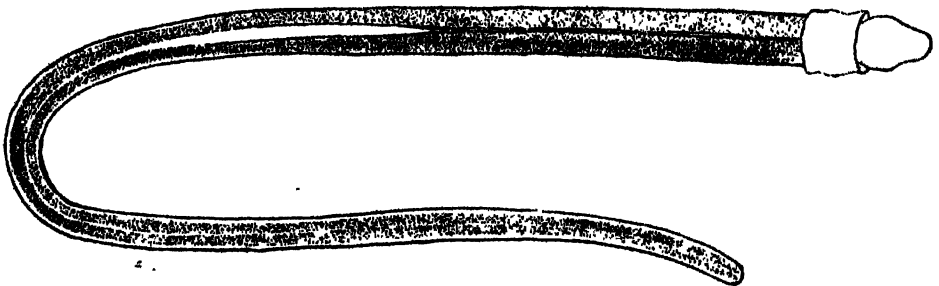
*Ptychodera capensis.*

FIG. 2.

*Ptychodera proliferans.*

transition from one form to the other was observed. The external differences between the two are shown diagrammatically by figs. 1 and 2, in which the bright yellow gonads are indicated by stippled shading and the hepatic caeca by black. Figs. 3 and 4 represent regenerating fragments, two and four weeks respectively after breaking off from the parent.

As both species are hardy animals, thriving fairly well in captivity when supplied with abundant pure sea-water, a number were kept in small glass tanks partly filled with sand, and were examined from time to time. The

process of asexual reproduction was continuous in the summer months, but not rapid. In the case of half-a-dozen *P. proliferans*, kept in a separate vessel, about four to six small fragments were given off every week. For a time these remained in close proximity to the parent, but many of them were subsequently found free on the surface of the sand, and were readily moved about by any commotion of the water—probably a means of dispersal. Some of these fragments were isolated and examined from time to time. They moved about freely, a proboscis and traces of a collar appeared, and for three weeks seemed to be developing into a form like their parent *P. proliferans*, but, about the end of this period, some of them were seen to be developing hepatic cæca and genital wings, while still retaining the bright yellow colour and narrow intestine of the parent. Finally, after about a month, they had the general characteristics of *P. capensis*, with a few well-marked cæca and whitish caudal region, now containing a few grains of sand. The bright yellow colour had entirely disappeared even from the branchio-genital region, and they could not be distinguished from small *P. capensis* at a stage in which the gonads are not yet developed.

FIG. 3.



Proliferated part 14 days after  
separation.

FIG. 4.



Proliferated part 25 days after  
separation.

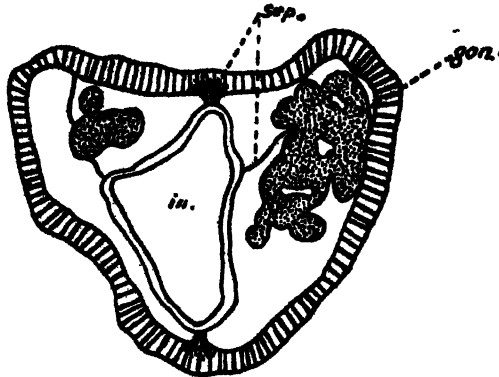
In order to ascertain further details of the transformation of the one form into the other, various stages were examined by sectioning. Sections of the tail region of *P. proliferans* show that the lateral septa are well developed throughout its length, and are in intimate connection with the gonads, which contain eosinophil globules, and, in some cases, one or two ova. The same condition is, of course, found in the segments which break off from its posterior extremity, and this is maintained until the stage when the proboscis with notochord, &c., have appeared.

Figs. 5 and 6 show the conditions in a segment in which the proboscis is clearly shown, but not the collar region, and the gonads occur, not as a continuous streak, but at intervals, so that in some sections (fig. 5) the gonads still occupy a large part of the body cavity, but a few sections further on (fig. 6) they are almost entirely absent, though the lateral septa are still present. Sections of the same region at a later stage (about 4 weeks) (fig. 7) show an entire absence of gonads and no trace of lateral septa. Fragments of food-material—diatoms, protozoa, and flocculent organic matter—may now be seen in the intestine.

Evidently, therefore, the two species are identical, *P. proliferans* being capable of giving rise asexually to *P. capensis*. The question then arises as

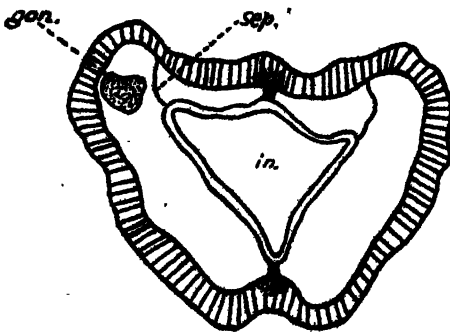
to whether this is a case of alternation of generations, *P. capensis* being the sexual form. To ascertain this the genital pleuræ of *P. proliferans* were examined by teasing, sectioning, and compression, the last-named method being the most suitable for examining a large number of individuals, as the ova are fairly large (.12 mm.) and conspicuous. The results of the examination were not consistent, some having apparently no ova, some only a few, and some a fair number.

FIG. 5.



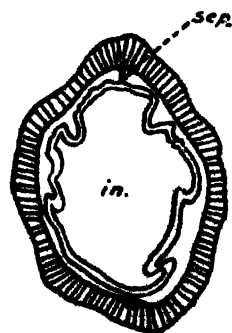
Transverse section of caudal region of the stage shown in fig. 3.  
gon. = gonads; in. = intestine; sep. = septum.

FIG. 6



Another section of caudal region  
further back than that shown  
in fig. 5.

FIG. 7.



Transverse section of  
caudal region at the  
stage shown in fig. 4.

Towards the end of the summer (May) the six *P. proliferans* kept under observation had become considerably reduced in size, and a change was observed. The posterior region of the body became of a paler colour, the yellow streaks being reduced to a few scattered patches, and the intestine

contained a few grains of sand. At a later date hepatic cæca appeared about the middle of the body, and subsequently all were transformed into typical *P. capensis*, with fairly well-developed gonads, in which, however, there were no ova. Thus both the parent and its proliferated parts ultimately assumed the form of *P. capensis*.

*Ptychodera proliferans* would seem, however, to be capable of reproducing sexually, as the gonads contain well-developed ova. The facts, however, that (1) ova may occur in the proliferated part, and be used up like the granules in the growth of the body, and (2) that the ova ultimately disappear in the reduced adult, seem to indicate that there is no sexual reproduction in this form. There can be little doubt that *P. capensis*, into which both buds and parent are transformed, reproduces sexually, so that the whole process looks like a modified form of alternation of generations. There is evidence, however, which seems to indicate that *P. proliferans* arises from *P. capensis* by a division of the latter in front of or at the hepatic region, and subsequent prolongation and proliferation of the genital region, followed finally by regeneration of the lost hepatic and caudal region.

The nutritive eosinophil globules or granules evidently play an important part in the life-history of the animal, and their relation to the sexual elements may therefore be further enquired into.

They have been noted in many other Enteropneusta, but their origin and function remain in doubt. Spengel found that, in *P. minuta*, they were contained in cells in which no nuclei were seen. In *P. flava* Willey found no normal nuclei, and believed that the nuclei of the cells undergo a process of degeneration analogous to fatty degeneration. They were found to be present when the germ-cells were fully developed, but both authors found that they disappeared at the period of complete sexual maturity in the species they examined. As to their functions, Spengel could come to no definite conclusion; Willey suggested that they are partly for the nutrition of the growing germ-cells, but principally for providing an albuminous covering to protect the germ-cells during maturation.

In *P. capensis* they are absent only in the young stages. They are present from the time the germ-cells begin to develop and increase in numbers with them, and are present when the animals are fully developed. They do not disappear at complete sexual maturity, though the sexual elements then preponderate, and they subsequently (towards the end of the winter, when exceptionally large specimens were found) appear to increase in number, their bulk greatly exceeding that of the remaining germ-cells.

In *P. proliferans* stage they constitute the main mass of the gonads. These are greatly attenuated posteriorly and occur, as already stated, as two narrow streaks of a bright yellow colour in the elongated posterior region of the body, which is rounded and without pleural ridges in the living animal. The relative abundance of ova and globules was ascertained by the methods

already stated, and it was found that the well-developed gonads consisted mostly of globules alone, the eggs being only present, and in diminished numbers, in some cases.

The functions of globules in this case seem obvious, namely, the sustenance and growth of the non-feeding *P. proliferans*, and of the buds, till they reached the feeding stage.

The origin of globules and ova may best be studied in sections of *P. capensis* at a stage when the gonads are beginning to appear as small yellow streaks in the genital wings, and their early stages may be seen at the extremities of their lobate ramifications. The gonads are surrounded with a layer of cells with elongate nuclei. The developing ova occur just within this layer. They are of irregular amoeboid shape, and the germinal vesicle is already well marked. Alongside of the ova, and apparently arising from the same peripheral epithelium, are other cells, the outlines of which are not well marked, containing lenticular nuclei like those of the outer layer, and numerous small globules. In the older parts of the gonads the globules constitute a solid mass, sometimes with many scattered and disintegrated nuclei, and, in still later stages, only a mass of globules, some small and some comparatively large, the latter being most probably formed by confluence of the smaller. No globules were seen in the body of the ovum, which, when mature, is surrounded by a zone of clear tissue with radiating lines. It appears to be a reasonable inference that the granules are produced by modified germ-cells.

Though no such process of asexual reproduction has apparently been observed in other members of the Enteropneusta, the tendency of some species to fragmentation and regeneration is well known, and, if their life-histories could be followed out, it might be found that reproduction by fission is not an unusual process of multiplication, and is associated with the great abundance of eosinophil globules, which otherwise seem so difficult to account for.

The presence or absence of hepatic caeca, as well as the extent of their development, has not been found of any great systematic value in the Enteropneusta, and this case may indicate that other species may at different times assume different forms, in which these structures may be absent, or in various stages of development as in *P. proliferans*.

Some ten years ago it was noted as a remarkable fact by Korschelt and Heider that, while asexual reproduction was such a characteristic feature of *Cephalodiscus*, it was entirely absent in the closely-allied *Balanoglossus* and in *Phoronis*. Since that date it has been shown by Harmer that it is a normal process in a species of *Phoronis*, so that this distinction between the Pterobranchia, Enteropneusta, and Phoronidea disappears.

On the Morphology of the Head Capsule and Mouth-parts of *Chlorops tæniopus* Meig. (Diptera). By J. G. H. FREW, M.Sc., Ministry of Agriculture Research Scholar. (From the Entomological Department, Rothamsted Experimental Station, Harpenden.) (Communicated by Dr. A. D. IMMS, F.L.S.)

(With 7 Text figures.)

[Read 3rd May, 1923.]

THE following paper deals with a part of the anatomical work done in connection with an investigation into the life-history and bionomics of the Gout-fly of Barley (*Chlorops tæniopus*) which is being carried on at Rothamsted under the direction of Dr. A. D. Imms. Considerable attention has recently been directed to the Dipterous head capsule owing to Peterson's valuable monograph on the subject (3), and as the results of the present investigation seem to necessitate important modifications of some of the homologies put forward by Peterson, it has been thought advisable to deal with the morphology of the head capsule of *Chlorops* in a separate paper. Peterson's nomenclature is followed in all cases unless there is very strong evidence that it is incorrect.

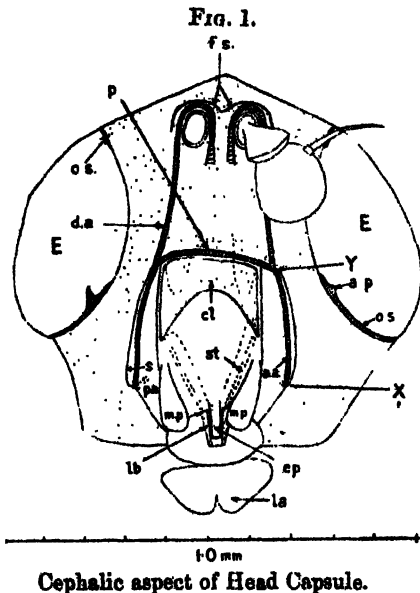
#### THE TENTORIUM AND THE EPICRANIAL SUTURE.

The location of the epicranial suture is of fundamental importance in determining the homology of the regions of the head capsule, and the position of the invaginations of the arms of the tentorium is, in cases of doubt, the safest guide to the position of the epicranial suture. The epicranial suture is typically A-shaped. The stem represents the line of junction of the paired sclerites of the head, while between the arms lie the unpaired sclerites, the frons, clypeus, and labrum. Except in a few forms (Peterson, p. 15) the stem of the epicranial suture is wanting in Diptera. The tentorium consists of an arrangement of chitinized rods and plate-like structures. These arise from three pairs of invaginations on the head—the openings of the posterior, anterior, and dorsal arms of the tentorium. The invaginations of the posterior arms are situated one on each side of the occipital foramen and are joined by a transverse chitinous bar, forming the body of the tentorium and dividing the occipital foramen into dorsal and ventral halves. "The invaginations of the anterior arms are usually associated with the lateral margins of the clypeus, with one of the points of articulation of the mandibles, and frequently with the ventral ends of the arms of the epicranial suture. The invaginations of the dorsal arms are associated with the points of attachment of the antennæ

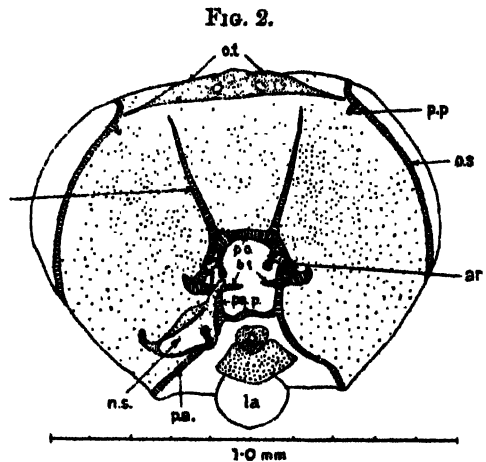


and near the dorsal portions of the arms of the epicranial suture" (Peterson, p. 26). According to Comstock and Koochi (1, p. 41), "Each dorsal arm of the tentorium arises from the side of the body of the tentorium between the anterior and posterior arms, and extends either to the front or to the margin of the antennal sclerites."

If one examines the tentorium of *Chlorops* it is seen to consist of three distinct chitinous rods on each side (figs. 1 and 2). One rod on each side (*p.a.*) arises at the side of the occipital foramen and passes forwards along the ventral surface of the head capsule ending at the point marked X in figure 1, at the ventral corner of the ridge which forms the lateral boundary of the oral depression in which the proboscis lies when retracted. These two rods are obviously the posterior arms of the tentorium; the question



Cephalic aspect of Head Capsule.

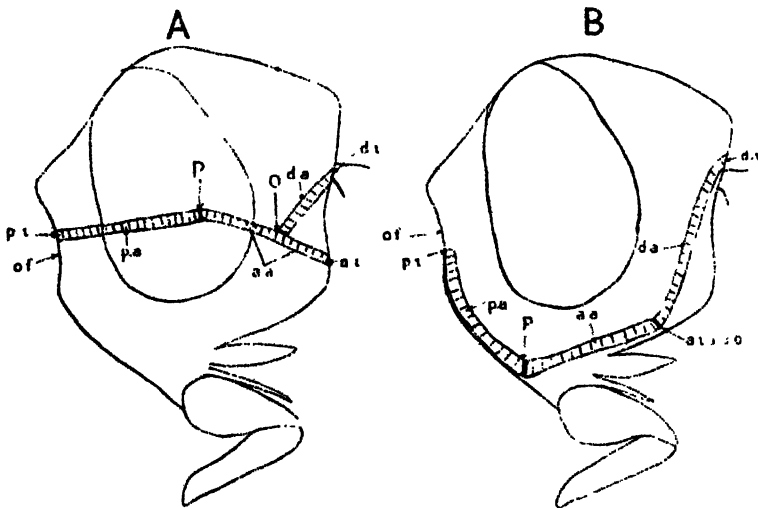


Caudal aspect of Head Capsule.

of the position of the body of the tentorium is dealt with in connection with the morphology of the caudal aspect of the head. From the point X a second chitinous bar (*a.a.*) runs along each lateral margin of the oral depression ending at the point marked Y in the figure. This bar is a thickening of the mesial wall of a shallow slit-like depression (*s.*), which extends along each lateral margin of the oral depression. From the point Y a third bar (*d.a.*) on each side extends dorsally along the anterior surface of the head; the dorsal end of each of these bars is strongly curved and almost encloses the antennal base of its side in the manner shown in the figure. All three arms of the tentorium are fused along their entire length with the head capsule. The dorsal margin of the oral depression is marked by a strong bar (*p.*), which unites the two halves of the tentorium.

It seems clear that the bars extending from the points Y to the antennal bases are the dorsal arms of the tentorium, and their antennal ends are probably to be regarded as their points of invagination. The bars on each side uniting the points X and Y are here regarded as the anterior arms of the tentorium, their dorsal ends (Y) being their true points of invagination. As already mentioned, their invaginations are actually slit-like and extend along their whole length. Peterson has described several *Brachycera* and *Cyclorrhapha* *Aschiza* in which similar, though apparently not such pronounced, slit-like invaginations run along the anterior arms of the epicranial suture, and the occurrence of slit-like invaginations in *Chlorops* cannot, therefore, be regarded as in any way exceptional. It thus seems clear that the three arms of the tentorium can be recognized in *Chlorops* as in less

FIG. 3.

Diagram illustrating the nature of the tentorial thickenings of *Chlorops*.

specialized insects, though their relations to each other are undoubtedly very different from the relations in more typical tentoria. Peterson, speaking of generalized insects, says (p. 26): "The small dorsal arms unite with the larger anterior arms, and these, in turn, join with the posterior arms." Fig. 3 A represents this diagrammatically; the points O and P represent respectively the points of junction of the dorsal arms with the anterior arms, and of the latter with the posterior arms. Fig. 3 B represents diagrammatically the condition found in *Chlorops*, and the following provisional explanation is offered. In *Chlorops*, as in most species possessing a ptilinum, the rods of the tentorium have become fused with the head capsule. In the case of the anterior arm this may be supposed to have resulted in the entire obliteration of the portion of the rod extending from a.i. (its point of invagination) to O,

so that these two points become coincident, the anterior arm now being represented only by the portion between the points O and P. Although this explanation seems quite plausible, an examination of Peterson's extensive series of figures has failed to reveal any morphological evidence in support of it in the shape of intermediate forms, and in view of the extensive series of forms studied by Peterson it seems unlikely that such evidence is available.

Peterson (p. 16), although he says that the anterior arms of the epicranial suture are not present in any Dipteron possessing a ptilinum, considers, nevertheless, that "there is every reason to believe that the tentorial thickenings mark the course of the suture." If one accepts this view the region of the head lying between the dorsal arms of the tentorial thickenings in *Chlorops* must be the frons; but owing to the curved dorsal ends of the thickenings the antennæ arise, quite definitely, on this included region. Such a position for the antennæ does not occur, so far as I know, in any insect, and one must, therefore, conclude that the region lying between the dorsal arms of the tentorial thickening is not the frons (or fronto-clypeus).

I consider that the tentorial thickenings between the points X and Y on each side mark the lower portions of the arms of the epicranial suture, the shallow invaginations in which the thickenings lie being probably the actual sutures which have remained permanently open. As mentioned above, the dorsal edge of the oral depression is formed by a transverse chitinous bar uniting the two halves of the tentorium, and I consider that this represents the dorsal and median region of the arms of the epicranial suture. The following passage from Peterson (p. 28) gives, I think, considerable support to this view. Speaking of the invaginations of the anterior arms of the tentorium in *Tubanus* he says:—"The invaginations on each lateral half of the head are joined together by the arms of the epicranial suture and resemble the hypothetical type." The points Y have already been indicated as probably representing the points of invagination of the anterior arms of the tentorium.

I consider, therefore, that the dorsal and lateral margins of the oral depression coincide with the anterior arms of the epicranial suture. According to this view the antennæ arise on the vertex, a position which they occupy in many Orthorrhapha, and one must look for the frons and clypeus among the structures lying in the oral depression. On the dorsal surface of the rostrum of the proboscis there is a plate which is the superficial region of a chitinous structure usually termed the fulcrum. Lowne (p. 134) regarded this as the clypeus, and Dr. Imms tells me that he is expressing the same view in a forthcoming publication. With this view I agree, with the small reservation that, as according to Peterson (p. 17) the frons and clypeus are separated by a doubtful suture in only a few Orthorrhapha\* and are entirely fused in the majority, it is possible that the sclerite in question

\* He also regards the frons and clypeus as fused in the Cyclorrhapha, but here the region which he calls fronto-clypeus is, in my opinion, part of the vertex.

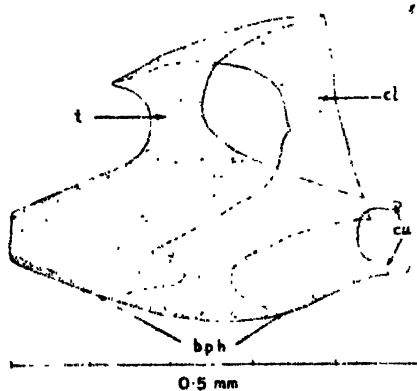
represents the fronto-clypeus. If it only represents the clypeus, the frons is represented by the intervening membrane uniting it to the dorsal edge of the oral depression.

Only in *Mycetophila* among the Dipterous types studied by Peterson is the stem of the epicranial suture complete. Some forms (*Rhabdophaga*, *Mycetobia*, *Tabanus*) "show depressions or thickenings along the meson. These marks may have no significance" (p. 15). In *Chlorops* there is a very distinct internal ridge running along the meson from the median ocellus to the median point of the dorsal edge of the frontal suture.

#### TORMÆ AND FRONTO-CLYPEUS.

In the base of the rostrum there is a somewhat complex chitinous structure usually termed the fulcrum (fig. 4), part of which is internal and is formed by the chitinized basipharynx, and part of which is superficial and is, as stated above, the clypeus or fronto-clypeus. The internal portion will be

FIG. 4.



Ventro-lateral view of basipharynx, tormæ, and clypeus.

considered later; it consists of dorsal and ventral plates enclosing between them the pharyngeal cavity. A vertical chitinous plate (*t*) on each side unites one side of the superficial plate (clypeus) to the corresponding side of the basipharynx. Peterson regards these, together with the superficial plate which I consider to be the clypeus (or fronto-clypeus), as the Tormæ.

"The tormæ in generalized insects are chitinized pieces which belong to the lateral portions of the epipharynx in the region of the clypeo-labral suture and connect with the clypeus or labrum at the lateral ends of the suture. . . . The tormæ of generalized Diptera also connect with the inner surface of the ventral portion of the fronto-clypeus" (Peterson, p. 19). The basipharynx is composed of united epipharynx and hypopharynx. Thus, by accepting the view that the superficial plate is the clypeus or fronto-clypeus,

it will be seen that the lateral vertical plates have absolutely typical relationships as tormæ. According to Peterson's view that the lateral plates and the superficial plate represent tormæ alone, the tormæ of the Cyclorrhapha are strikingly different in their relationships from the tormæ of generalized insects or of the Orthorrhapha; a difference which he hardly attempts to explain.

As in the remainder of this paper I shall have no cause to disagree with Peterson's views, it may be useful to summarize here the points of difference. In *Chlorops* I consider that the tentorium clearly consists of the three typical arms; this may, however, be a special case, as it certainly appears to be judging from Peterson's figures, and not general to all Cyclorrhapha. The following points, however, are almost certainly applicable to all Cyclorrhapha:—

1. The position of the arms of the epicranial suture is marked by the dorsal and lateral borders of the oral depression.
2. All regions of the head lying dorsal and lateral to the oral depression are derived from the paired sclerites of the head, and the frons and clypeus must lie within the oral depression.
3. The antennæ arise on the vertex.
4. The superficial plate of the fulcrum is the clypeus or fronto-clypeus.
5. The tormæ are the chitinized plates joining the sides of the clypeus to the sides of the chitinized basipharynx.

It cannot be claimed that absolutely rigid proof of any one of the above statements has been given. The evidence in support of them seems to me, however, to be very strong, and their acceptance appears to afford a very much clearer explanation of the nature of the facial aspect of the Cyclorrhaphous head capsule than does Peterson's homology, and, moreover, brings the Cyclorrhaphous head capsule more into line with that of the Orthorrhapha or of generalized insects.

The *Ptilinum* shows no marked peculiarities. It lies within the head capsule close against its anterior wall. The frontal suture (*f.s.*) lies just dorsal to the antennal bases.

The *Labrum* (figs. 1, 5, & 6) is a rather heavily chitinized triangular sclerite lying along the dorsal surface of the mediproboscis, its base being continuous with the dorsal membrane of the distal end of the basiproboscis, so that it is separated from the clypeus by a considerable extent of membrane—a condition which is usual, but not universal, in Diptera (Peterson, pp. 20–21). The ventral surface of the labrum is longitudinally grooved for the reception of the epipharynx, which fits tightly within the groove and cannot be removed without damaging the labrum. The epipharynx does not extend quite to the distal end of the labrum, and just beyond its termination the labral groove bears two small conical papillæ, one on each side, which have

the appearance of being sense-organs. The dorsal surface of the labrum is strongly convex from side to side; its base articulates with the distal ends of the stipites (fig. 6). The labrum, together with the epipharynx, is easily lifted from the surface of the proboscis and rotated dorsally, its base hinging on the stipites.

*The Vertex* "is interpreted as including all the cephalic and dorsal aspects of the epicranium except the front. . . . The region of the vertex ventrad and mesad of each compound eye is a gena" (Peterson, pp. 21-22). It is only necessary to remark that what Peterson calls the front is, in my opinion, part of the vertex. The term "front" as applied to *Cyclorrhapha* has no true morphological significance, but the region defined by the term is so well understood, and the term is so constantly used in taxonomical writings on Diptera, that it would, I think, be a mistake to propose any new name for this region.

*The Compound Eyes and Ocelli*.—The only noteworthy feature concerning the eyes is the presence round their margins of a well-marked, though incomplete, ocular sclerite (figs. 1 & 2, *o.s.*). This ring sclerite is incomplete anteriorly; it bears two small peg-like projections, an antero-ventral (*a.p.*) and a postero-dorsal (*p.p.*). The three ocelli are situated on the vertex some distance dorsal to the frontal suture, and lie on a raised and dark-coloured triangular area (fig. 2, *o.t.*), which is continued forwards in front of the median ocellus as a dark-coloured internal chitinous ridge running along the median line of the vertex and ending at the dorsal margin of the frontal suture.

#### OCCIPUT AND POSTGENÆ.

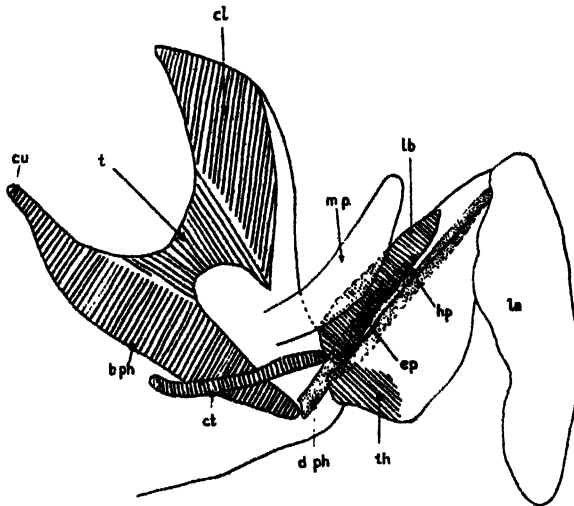
Owing to the absence of sutures on the caudal aspect of the head (fig. 2), it is not possible to define with certainty the limits of the occiput and postgenæ, and accordingly Peterson's view is followed that all regions of the caudal aspect lying dorsal to a transverse line drawn through the middle of the occipital foramen belong to the occiput, while the areas ventral to this line and lateral to the mesial membranous area are the postgenæ. The dorsal half of the foramen is strengthened by a thickening of the occiput (*p.o.*) which provides articulation for the neck sclerites. I follow Peterson in calling this the Parocciput. It is not marked off from the occiput by a secondary suture, as is frequently the case in Diptera. On each side a chitinous peg (*b.t.*) projects mesially across the foramen, the two almost meeting in the median line and dividing the foramen into dorsal and ventral halves. These certainly appear to me to be processes of the ventral ends of the parocciput, but Peterson has named apparently identical structures (*e.g.* in *Chloropis glabra*, fig. 132) as the body of the tentorium, and as he has examined a large series of forms and has therefore had the opportunity of tracing the variation of the body of the tentorium in Diptera, I have decided to follow

his nomenclature in this matter. On each side the parocciput bears an articular surface of somewhat complicated nature (*art.*) with which the anterior end of the chief neck sclerite on each side articulates.

The ventral half of the rim of the occipital foramen is thickened (*pa.p.*), and the posterior arms of the tentorium appear to arise from this thickened rim. This is the Parapostgenal thickening (Peterson, p. 24).

Two long chitinized ridges (*r.*) occur on the inner surface of the occiput, one on each side, arising from the dorso-lateral region of the parocciput and extending dorso-laterally towards the eyes. A median thickening, which is present in many *Cyclorrhapha* in addition to the above, is not found in *Chlorops*.

FIG. 5.



Lateral view of the proboscis.

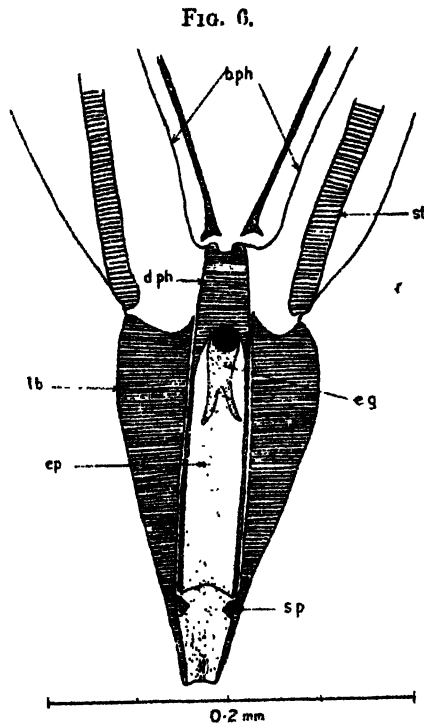
The *Antennae* consist of three basal joints and an arista arising from the third joint and itself three-jointed. The second joint of the antenna has a cone-shaped apex which fits into the base of the third joint. The basal joint is a ring-shaped sclerite and is united to the second joint by a membranous region of considerable extent. There is a relatively large pit on the under surface of the third joint which is probably a sense-organ, but which has not yet been closely examined. The arista is minutely pilose.

*Mandibles* are absent.

The *Labium* forms the greater part of the proboscis. The following is a brief *résumé* of Peterson's views on the homology of the Dipterous proboscis:—The membranous basiproboscis is made up of submentum, mentum,

and the cardines and stipites of the maxillæ, but the limits of the sclerites cannot be distinguished. The mediproboscis and the distiproboscis constitute the ligula. The labellæ are the paraglossæ, and between them are two membranous lobes which are the glossæ\*.

In the membranous basiproboscis of *Chlorops* only the stipites (figs. 1, 5, 6, *st.*) can be distinguished as separate sclerites. In the majority of Cyclorrhapha a distinct galea is found attached to the ventral end of each stipes, part of it appearing on the surface of the proboscis (the stipites lying



Ventral view of labrum, epipharynx, and associated parts.

entirely within the proboscis). "In the Calypteratæ and some of the Acalypteratæ the galea articulates with the proximal end of the labrum and is more or less firmly connected with the same. The ectal exposure of the galea is very small in these forms" (Peterson, p. 41). In *Chlorops* I have been unable to differentiate the galeæ, and they have probably fused with the

\* Other views on the morphology of the proboscis are given by Wesche, W., "The Labial and Maxillary Palps in Diptera" (Trans. Linn. Soc., Zool. vol. ix. 1903-7), and by Crampton, G. C., "The Sclerites of the Head, and the Mouth-parts of certain Immature and Adult Insects" (Ann. Ent. Soc. Amer. vol. xiv., 1921). The former author considers that the palpi of Muscidæ are labial and not maxillary. Crampton considers that the labella of Diptera are labial palps.



ventral end of the stipites, which, as already mentioned, articulate with the base of the labrum. Although very near the surface I could not definitely determine that any part of these ventral ends was actually superficial. The stipites are flexible, and probably springy rods. When the proboscis is extended they are practically straight, but they are considerably curved when the proboscis is retracted. They probably assist in the extension of the proboscis by pressing on the base of the labrum; this point, however, requires further investigation. According to Peterson the areas mesad of the stipites are to be considered as developed from the submentum and mentum, while the areas lateral to them are formed from the maxillæ.

The *Theca* (fig. 5, *th.*) is a broad curved sclerite lying on the caudal aspect of the mediproboscis. It is not very heavily chitinized, nor are its limits very sharply defined. On its dorsal (anterior) aspect the mediproboscis is channelled by a longitudinal groove whose walls are rather more heavily chitinized than the general membrane of the mediproboscis; the hypopharynx lies in this groove.

FIG. 7.

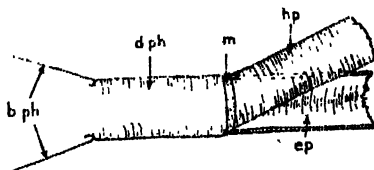


Diagram of the relationship of the epipharynx and the hypopharynx. (Ventral view.)

The *Labellæ* (Paraglossæ) are shown in fig. 5. A detailed account of their structure is unnecessary as they are essentially similar to those of *Musca*. Each labella forms half of the stomal disc, the two being united mesially by a flexible membrane, and each bears three pseudotracheæ. The two outer pseudotracheæ of each side unite to form a short common duct which opens into a short but wide groove at the proximal end of the stomal disc, this groove being continuous proximally with the groove of the hypopharynx. The mesial pseudotrachea of each side opens separately into the short common groove. The glossæ cannot be distinguished. According to Peterson this is also the case in *Chloropisca*, where "it is impossible to differentiate the glossæ from the chitinized groove of the mediproboscis and the proximal ends of the pseudotracheæ" (p. 49).

In the majority of Diptera each paraglossa is supported by a triradiate chitinized rod—the *Furca*—lying on its lateral and caudal aspects, and in the majority of Brachycera and Cyclorrhapha there is a small sclerite—*Sigma*—situated between each furca and the ventral margin of the theca. Neither of these sclerites is present in *Chlorops*, but this is not very surprising, as Peterson mentions a number of Diptera, *Chloropisca* among them, in

which he has been unable to distinguish them. "Kappa" is also absent, but Peterson has only found this sclerite in *Tabanus*, *Tipula*, and *Bittacomorpha*, where it lies "embedded in the membrane laterad of the ventral ends of the theca."

The *Maxillary Palps* (*m.p.*) are one-jointed and present no peculiarities.

#### EPIPHARYNX AND HYPOPHARYNX.

The epipharynx (*ep.*, figs. 1, 6, 7) lies in the groove on the under side of the labrum and is in the form of a gutter, semicircular in cross-section and opening ventrally. The hypopharynx (*hp.*) is a similar but rather more delicate structure lying in the groove on the dorsal surface of the mediproboscis, its opening facing dorsally so that, when epipharynx and hypopharynx are in contact, a closed hollow cylinder of chitin is formed. At about the point of junction of mediproboscis and distiproboscis the epipharynx and hypopharynx unite to form a short closed cylindrical tube, the distipharynx (*d.ph.*), whose proximal end articulates with the distal end of the basipharynx (*b.ph.*), the cavities of the two being continuous. Although it is certain that the short distipharynx consists of united epi- and hypopharynx, it has the appearance of being formed by the former alone, which is obviously a direct continuation of it, whereas the hypopharynx is separated from the distipharynx by a narrow membranous area acting as a hinge, and is easily broken off at this point.

Just distal to its junction with the distipharynx the epipharynx has a rather deep groove (*ep.*, fig. 6) on its surface. The hypopharynx apparently lies quite freely in the groove on the mediproboscis, from which it is easily detached except at its distal end, where the two are united. As the labrum is slightly, and the epipharynx considerably, shorter than the hypopharynx, there is a short distal region of the latter which cannot be converted into a closed groove by the apposition of the labrum or epipharynx. The distal end of the hypopharyngeal groove is, however, deep, and a study of serial sections has afforded some evidence of the possibility of the lips of the groove being brought together to form a closed channel, such a closure being probably effected by an increase of turgidity in the mediproboscis due to the pumping in of body-fluid when the proboscis is extended for feeding.

#### BASIPHARYNX. (Figs. 4 & 5, *b.ph.*)

The form of the basipharynx is sufficiently well shown in the various figures. It is an organ of suction. Muscles arise from the dorsal surface of the basiproboscis and are inserted into the dorsal wall of the basipharynx, which they raise by their contraction, thus increasing the capacity of the pharynx. Posteriorly the basipharynx ends in two blunt cornua (*cu.*). Peterson interprets the basipharynx as consisting of united epipharynx and hypopharynx.

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- (2) LOWNE, B. T. (1890-95). "Anatomy, Physiology, Morphology, and Development of the Blow-Fly." London.
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*Index lettering to Text-figures*

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|--|--|
| <i>a.a.</i> , <i>d.a.</i> , and <i>p.a.</i> anterior, dorsal, and posterior arms of the tentorium. | <i>n.s.</i> neck sclerite.   |
| <i>a.i.</i> , <i>d.i.</i> , and <i>p.i.</i> their points of invagination.                          | <i>O.</i> point of junction of dorsal and anterior arms of the tentorium.    |
| <i>a.p.</i> antero-ventral process of ocular sclerite.   | <i>o.f.</i> occipital foramen.   |
| <i>art.</i> articular surface for neck sclerite  | <i>o.s.</i> ocular sclerite.   |
| <i>b.ph.</i> basipharynx.  | <i>o.t.</i> ocular triangle.   |
| <i>b.t.</i> body of the tentorium.   | <i>P.</i> point of junction of anterior and posterior arms of the tentorium. |
| <i>cl.</i> clypeus.  | <i>p.</i> thickening of dorsal margin of oral depression.                    |
| <i>cu.</i> cornu of basipharynx.   | <i>pa.p.</i> parapostgenal thickening.                                       |
| <i>d.ph.</i> distipharynx.   | <i>p.o.</i> parocciput.  |
| <i>E.</i> compound eye.  | <i>p.p.</i> postero-dorsal process of ocular sclerite.                       |
| <i>e.g.</i> epipharyngeal groove.  | <i>r.</i> ridge on occiput.  |
| <i>ep.</i> epipharynx.   | <i>s</i> slit-like invagination containing anterior arm of tentorium.        |
| <i>f.s.</i> frontal suture.  | <i>s.p.</i> sense (?)-organ on labrum.                                       |
| <i>hp.</i> hypopharynx.  | <i>st.</i> stipes.   |
| <i>la.</i> labellum.   | <i>t.</i> toima.   |
| <i>lb.</i> labrum.   | <i>th.</i> thinn   |
| <i>m.</i> membrane separating hypopharynx from distipharynx.                                       |  |
| <i>m.p.</i> maxillary palp.  |  |

## The Crustacean Plankton of the English Lake District.

By ROBERT GURNEY, M.A., F.L.S.

(PLATE 23 and 3 Text-figures.)

[Read 3rd May, 1923.]

THE published information with regard to the Crustacea of the Lake District is surprisingly scanty. Mr. Scourfield has included all available records in his *Synopsis of British Entomostraca* (1903-4), but naturally dealt only with the district as a whole, without comparison of the fauna of the different lakes. Miss Pratt's paper on the Entomostraca of Lake Bassenthwaite is the only attempt that has been made to give a comprehensive account of the Crustacea of any single lake. The phytoplankton, on the other hand, is fairly well-known as a result of the work of Messrs. West and of Dr. Pearsall.

The following account of the Crustacea of the district lays no claim to being exhaustive or even to deal with many of the points of special interest, but at least it may serve as a groundwork for comparison with other lake areas and to draw attention to questions on which further work is required.

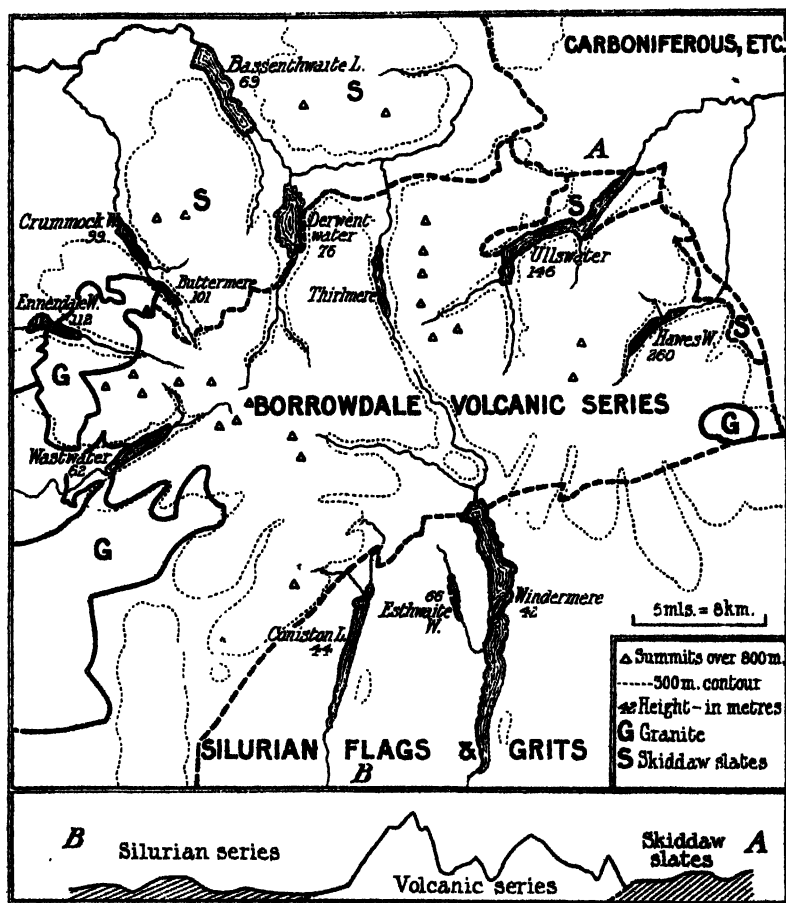
The material at my disposal consists chiefly of a series of plankton samples taken by Dr. W. H. Pearsall during 1921 and 1922 for the purpose of a study of the phytoplankton, and I wish to express my thanks to him for the loan of these collections and for the valuable information which he has readily given to me during the course of the work. I have also myself visited the district and have made collections in a few of the lakes. During the autumn of 1922 I spent a week in the western part of the district specially investigating the Crustacea of Ennerdale, Wastwater, and Coniston.

While it is probable that the collections at my disposal give a fairly complete picture of the composition of the crustacean plankton of the various lakes, it is unfortunately true that the methods which are suitable for the collection and preservation of phytoplankton are by no means so for the Crustacea; and for this reason, though Dr. Pearsall's collections extend over a large part of two years, it is not possible to deduce from them any reliable conclusions as to the seasonal distribution and variation of the Entomostraca.

Undoubtedly much further work remains to be done with regard to these two questions, and also in connection with the vertical distribution of the species. It seems also to be probable that the distribution of the Crustacea may not be uniform in some of the larger lakes, and that such lakes should not, therefore, be dealt with as homogeneous units. For instance, the composition of the plankton in the deep part of Ennerdale is not the same as

that of the shallow western part, and the same may be the case with Ullswater, Windermere, and, perhaps, Coniston. *Holopedium gibberum* was not found in any of Dr. Pearsall's collections from Windermere, but it was taken there many years ago by Beck, and again in 1912 by Mr. P. A. Buxton. It may be that it is a permanent inhabitant of the lake, but it is restricted to certain parts of it.

FIG. 1.



Map of the English Lake District, with section showing the relation of scenery and gradients to the underlying rocks.

(By permission of Dr. W. H. Pearsall and the Council of the Royal Society.)

I have thought it well to add notes on some of the species composing the plankton, and on the fauna of some of the high-lying lakelets or tarns, in order to give a more complete picture of the crustacean fauna than would be conveyed by a statement of the composition of the plankton alone.

With the physical conditions of the district and its lakes it is not my business to deal. The foundation of our knowledge of these lakes was laid in the survey of Dr. H. R. Mill (1895), and Dr. Pearsall has, in his papers on the aquatic flora and phytoplankton, added greatly to our knowledge of the post-Glacial history and present conditions of these lakes. The accompanying map clearly shows relations of the lakes, which occupy valleys radiating from a common centre.

THE PLANKTON.—*Comparison of the various Lakes.*

One of the chief results of Dr. Pearsall's work is that "the stage of evolution of the lake-basin must be regarded as being the fundamental factor affecting the distribution of the phytoplankton, since it is upon this factor that the character of the waters depends" (1921, p. 279), and he has divided the lakes into groups on the basis of the amount of silting of their beds. These groups are:—

I. Primitive Lakes.

Wastwater, Ennerdale, Buttermere, and Crummock.

II. Intermediate Lakes.

Hawes Water, Derwentwater, Bassenthwaite.

III. Evolved Lakes.

Coniston, Windermere, Ullswater.

IV. Most evolved Lakes.

Esthwaite (and Grasmere).

The phytoplankton corresponds fairly well with this grouping, the lakes of the first group containing a Desmid plankton, while in the remainder there is a large proportion of Diatoms. But Desmids are also frequent in Group II., while Myxophyceæ form an increasing component of the plankton of Groups III. and IV., and are at times dominant in Esthwaite. As Dr. Pearsall intends to deal in detail with the plankton as a whole in relation to its environment, I shall do no more than attempt to show how far the distribution of Entomostraca conforms to this grouping.

Any grouping of these lakes on the basis of their Crustacea is by no means easy, since, with the exception of Buttermere and Crummock, which lie in the same valley and undoubtedly at one time formed a single lake, each lake has its own individual character—so much so that it would probably always be possible to identify the lake from which any given representative sample of plankton was taken.

In Table 1, I have arranged the lakes in the groups adopted by Dr. Pearsall, Group I. being the most primitive and least silted, and from this table the composition of the Crustacean plankton can be seen at a glance. Every plankton species taken is recorded in the table, but those which occurred only singly in one collection or were evidently not regular constituents of the plankton are distinguished by a cross enclosed in a circle.

TABLE 1, showing composition of Plankton. The Lakes are arranged in Groups as in Pearsall, 1921, p. 276. Crosses enclosed in circles indicate that the species is occasionally found, but is not a regular member of the plankton. These species are not included in the total numbers.

	Group I.				Group II.			Group III.			Group IV.	
	Wastrer.	Funderdale.	Buttermere.	Crummock.	Hawes Water.	Derwentwater.	Bassenthwaite.	Coniston.	Windermere.	Ullawater.	Feshwaite.	Grasmere.
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Sida crystallina</i> .....	..	⊕	..	..	..	+	+	..	..	..	+	+
<i>Diaphanosoma brachyurum</i> .....	⊕	..	⊕	..	+	+	+	..	+	..	+	+
<i>Holopedium gibberum</i> .....	..	+	..	..	..	..	..	..	⊕	+	..	+
<i>Daphnia hyalina</i> s. str. ....	..	..	+	+	..	..	..	..	..	..	..	..
<i>lacustris</i> .....	..	..	..	..	+	+	..	..	..	..	+	..
<i>galeata</i> .....	..	..	..	..	..	..	..	+	+	+	..	..
<i>Ceriodaphnia</i> { <i>pulchella</i> .....	..	..	..	..	..	..	..	⊕	+	..	+	..
<i>quadrangula</i> } .....	..	..	..	..	..	..	..	..	..	..	..	..
<i>Bosmina longirostris</i> .....	..	..	..	..	..	..	..	..	..	..	+	+
<i>obtusirostris</i> .....	+	+	..	+	+	+	..	+	+	+	+	+
<i>Polyphemus pediculus</i> .....	⊕	..	..	⊕	⊕	+	+	..	..	..	+	..
<i>Bythotrephes longimanus</i> ..	+	+	..	+	+	+	+	+	+	+	..	+
<i>Leptodora kindti</i> .....	+	..	..	..	..	+	+	+	+	..	+	+
<i>Limnocalanus macrurus</i> ..	..	+	..	..	..	..	..	..	..	..	..	..
<i>Diaptomus laticeps</i> .....	..	..	..	..	+	..	..	..	..	..	..	..
<i>gracilis</i> .....	+	+	+	+	+	+	+	+	+	+	+	+
<i>Cyclops leuckarti</i> .....	..	..	..	..	..	+	+	..	+	..	+	..
<i>abyssorum</i> .....	+	..	+	+	+	..	..	+	+	+	..	+
Number of species .....	5	5	3	5	7	9	7	6	9	6	10	8

It should be noted further that collections have only been taken from the shore of Buttermere, and that I have only a single collection from Grasmere, taken in September 1912. Species which are known to belong to the littoral fauna, such as *Alonopsis elongata*, are omitted even when they have sometimes been taken in the plankton. *Chydorus sphaericus*, which is often limnetic in central European lakes, is not found in the plankton of this district.

It will be seen at once that the Crustacea do not conform to Dr. Pearsall's grouping, and indeed it is difficult to trace definite relationships at all.

Group I. of the lakes of the deep and rocky type agree in the limited number of species and the absence of species characteristic of shallow and warm waters, and in their predominant zooplankton, while Ennerdale and Wastwater together differ from Buttermere and Crummock in the entire absence of *Daphnia*. Buttermere and Crummock are characterized by the dominance in their plankton of the typical form of *Daphnia hyalina*. But, although Ennerdale and Wastwater are so alike in physical characters, they differ markedly in their plankton, not only in the species found, but in their relative abundance. Ennerdale possesses two striking species, *Holopedium gibberum* and *Limnocalanus macrurus*, which are absent from Wastwater, but, on the other hand, lacks both *Leptodora kindtii* and *Cyclops abyssorum*, both of which are common in Wastwater. Further, *Bosmina obtusirostris* is abundant in Wastwater, while it is an insignificant component of the plankton of Ennerdale. It cannot, in fact, be said that the Crustacea indicate any greater relationship between these two lakes than between either of them and certain lakes in other groups such as Hawes Water, Ullswater, or Conistone. In these two lakes Dr. Pearsall's grouping is put sharply to the test, for, so far as physical conditions go, two lakes could hardly be more alike than these, and their phytoplankton also is very similar.

The same difficulty is met with in the other groups, though it is true that Esthwaite has characters which distinguish it very clearly. It has a very varied plankton, which contains the "warm-water" or lowland Crustacea *Diaphanosoma brachyurum*, *Ceriodaphnia*, and *Cyclops leuckarti*; but its chief claim to distinction is the presence (in company with *B. obtusirostris*) of *Bosmina longirostris*, which is a distinctly southern form. Grasmere, except for containing *Holopedium*, is very similar to Esthwaite.

In Group II. it is clear that Hawes Water cannot be classed with Derwentwater and Bassenthwaite with regard to their Crustacea. The presence of the northern species *Diaptomus laticeps* places it in a class apart, its elevation of 694 feet giving it almost a position among the mountain tarns. It differs also from the other two, possibly for the same reason, in the different race of *Daphnia* inhabiting it, and also in the absence of *Sida*, *Leptodora*, and *Cyclops leuckarti*.

Derwentwater and Bassenthwaite also differ considerably, though forming part of one drainage system, for the latter lacks any species of *Daphnia* or of *Bosmina*, being unique among the lakes in this respect. It is true that both have been recorded from it, and that a single specimen of *Bosmina obtusirostris* occurred in one sample examined by me; but it is evident that, at the present time, neither can properly be included in its fauna. The great abundance of *Diaphanosoma* in the plankton of both lakes is a striking feature in common, and the plankton of Bassenthwaite may perhaps be regarded as that of Derwentwater, in which certain elements have been suppressed.



Dr. Pearsall suggests that the impoverishment of the plankton of Bussenthwaite may be due to the silt from lead mines washed into the lake during the past fifteen or twenty years. It is quite possible that to this cause is due the difference between the present plankton and the list given by Miss Pratt in 1898.

Group III. is also by no means a natural group from the point of view of the Crustacea, although the fact that it is only in the three lakes—Coniston, Windermere, and Ullswater—that *Daphnia* of the *galeata*-form occurs, may indicate a similarity of conditions. The presence of *Holopedium*, either regularly or occasionally, in Ullswater and Windermere may also be regarded as evidence of similarity, though the status of the species in the district is rather doubtful. It seems to me that, if any grouping is to be attempted on the basis of the crustacean plankton, Ullswater and Hawes Water should be included in the series of primitive lakes, while Windermere, with its *Diaphanosoma*, *Ceriodaphnia*, and *Cyclops leuckarti*, belongs more nearly to the Esthwaite-Grasmere series. Coniston, with its dominant crustacean plankton, comes near the primitive type, while Derwentwater and Bassenthwaite lead on towards the more evolved type of Windermere and Esthwaite.

It is impossible, without greatly extended knowledge of the food requirements of the Entomostraca, to determine what are the factors controlling their distributions in an area such as this. The evidence is conflicting. Birge (1898, p. 353) states that *Daphnia* feed readily on filamentous Diatoms (e.g. *Melosira*) and also on *Aphanizomenon* and *Anabæna*, while *Diaptomus* prefers *Anabæna* and *Aphanizomenon* to Diatoms. On the other hand, more recent investigations lead to the supposition that but little correspondence will be found between the distribution of the Entomostraca and the net phytoplankton, since the Entomostraca appear mainly to feed upon the minute nanoplankton, which is not taken in the plankton net. Woltereck (1908) stated that the net plankton is far too large to be taken in by *Daphnia*, their food consisting partly of the finest detritus, but mainly of the nanoplankton. The latter he found to be more abundant in the Lunzer Obersee, where *Daphnia* was more flourishing, than in the Untersee, and attributed this to the greater organic content of the water. This result was confirmed by experiment, since it was found possible to maintain limnetic *Daphnias* in health on a diet of a pure culture of *Chlorella*.

Naumann\* concluded that it was not the Algæ themselves but the detritus produced from them, and the smaller Flagellates, which provided the food for the Crustacea, and that the dust-fine organic detritus or peritripton, which may be introduced into the lake from without, may be of the utmost importance in the lime-free Palæozoic regions. In such lakes the zooplankton is greatly in excess of the phytoplankton. The lakes of the

\* I have not been able to consult Naumann's paper, but rely on a review of it in Arch. f. Hydrob. xii. 1920, p. 835.

lowlands of north and middle Europe are, on the other hand, rich in electrolytes, the phytoplankton is abundant, and the zooplankton feeds on the detritus derived from it.

Considerations such as these offer a possible clue to the understanding of the composition of the zooplankton, but leave untouched the problem of the distribution of the predaceous Cladocera such as *Leptodora*.

The factor which appears chiefly to influence the distribution of the Crustacea in this district is depth of water. A fair idea of the relative depth of the lakes is given by the following table, showing the percentages of the area covered by depths of 50 or 100 feet.

TABLE 2.—Depths of the Lakes. Figures from H. R. Mill, 1895.

	Maximum depth in feet.	Percentage of area covered by		
		0-50 feet.	0-100 feet.	over 100 feet.
Wastwater ..	258	23	39	61
Windermere ..	219	42	63·6	36·4
Ullswater ....	205	35·2	64	36
Conistone .. ..	184	37·1	60·8	39·2
Ennerdale .....	148	52·6	67·8	32·2
Crummock. . .	144	27	47	53
Hawes Water ..	108	61	98·3	1·7
Buttermere ....	94	37·8	100	—
Derwentwater .	72	93·9	100	—
Bassenthwaite .	70	94·1	100	—

In some cases this does not give a true impression, since, in the case of Ennerdale, Windermere, and Ullswater, there are deep and shallow basins. Mill divides the lakes into a deep and a shallow class, the latter including only Derwentwater and Bassenthwaite.

Now, the species of plankton Crustacea may be roughly arranged as Cold-water, Eurytherm, and Warm-water species, and it is found that the proportions in which these classes occur in the lakes vary in fairly close accordance with the depth. It should be noted that, in the following table, the lakes are arranged according to the percentage of depth over 100 feet, but Ennerdale is placed next to Wastwater, in view of the configuration of its eastern trough. Windermere and Hawes Water are more or less intermediate between the deep and shallow lakes in the character of the plankton,

but the former should be specially studied with a view to seeing if, as is probably the case, the plankton of the deep and the shallow basin differs in composition.

TABLE 3.—Composition of the Plankton.

	Cold-water Species	Eurytherm Species.	Warm-water Species.
Wastwater .	2	3	—
Ennerdale . .	3	2	—
Crummock	3	2	—
Conistone . . . .	2	1	—
Windermere . .	2	1	3
Ullswater . . . .	3	3	—
Hawes Water	3	3	1
Derwentwater .	1	5	3
Rassenthwaite .	—	1	3
Esthwaite . . . .	1	4	5

*The Northern Element in the Plankton.*

The general character of the plankton is very distinct from the Central European and Baltic types and resembles that of Scotland. Characteristic of it is the absence of *Daphnias* of the *racollata*-group and of *Bosmina longirostris* from all the lakes except Esthwaite and Grasmere, and of *Ceriodaphnia* from all but Windermere and Esthwaite.

The general abundance of *Bosmina obtusirostris* in itself marks the plankton as of the northern type, but the following species are also characteristic of northern or arctic lakes:—

*Holopedium gibberum.*

*Daphnia hyalina* s. str.

*Bythotrephes longimanus*

*Polyphemus pediculus.*

*Diaptomus laticeps.*

*Limnocalanus marinus.*

*Cyclops abyssorum.*

*Diaphanosoma brachyurum* may be looked upon as belonging to a southern, warm-water, genus, but it is itself so widely distributed throughout Europe, in cold as well as in warm waters, that little importance can be attached to

it in this connection. It is found only in the summer months and has an extremely short life-cycle, a fact which has probably largely assisted it to accommodate itself to a great variety of waters.

*Leptodora kindti*, although in deep lakes it may have a preference for the lower or colder strata, is by no means restricted to deep lakes, nor is it characteristic of northern regions. It may rather be regarded as a southern element in the fauna.

Although the crustacean plankton of the Lake District has a distinct northern facies, the absence from it of *Diaptomus laciniatus* and *D. wierzejskii*, which are not uncommon in Scotland, is noticeable. The latter is a eurytherm species of remarkably wide range, but characteristic of pools rather than of lakes, but the former is a definitely arctic-alpine species. *Diaptomus laticeps* is a member of the group of northern *Diaptomus* which is widely distributed in Scotland, but only occurs in this district in Hawes Water and Goats Water. It seems probable that it may be a recent immigrant.

From the point of view of the Crustacea the Lake District plankton certainly belongs to the Scottish Highland type, with the addition of a few southern forms.

It must be admitted that any discussion as to whether the plankton of any lake or district has a northern or southern facies is of doubtful value in the present state of our knowledge of the means of distribution and required conditions of existence of the different species. Not only is the whole question of the relation of the present fauna to the effects of the Glacial period far from being clear, but we have little means of knowing to what extent the fauna was able to survive that period in its original habitat. In the case of the Lake District it seems fairly certain that the present lake-basins were filled with ice, and it is probable that the whole district was covered with a mantle of ice, so that the present aquatic fauna is entirely of post-Glacial origin. It has been re-colonised largely by northern species, because these species find here, under a lowland climate, the conditions necessary for their existence, which are depth of water, form of lake-basin, and chemical composition of the rocks of the drainage area. The similarity of the plankton of the Scottish and Cumberland lakes, and of both with that of some Scandinavian and Irish lakes, may be due in large part to their being excavated in ancient lime-free rocks rather than to climatic influences. The similarity between the arctic and alpine fauna of Entomostraca may be accounted for by unlimited powers of dispersal rather than by the influence of the Glacial period. It is true that the evidence from other groups is in favour of the current views as to the relation of the alpine to the arctic fauna, but we require to know far more about means of dispersal before the matter can be regarded as decided. I will give two instances within my own knowledge which illustrate the danger of relying on limited powers of dispersal and upon the nature of the habitat in speculations regarding

post-Glacial distribution. In 1907 *Apus cancriformis*, which had not been seen in Britain for over 40 years, was found in Scotland by Mr. Balfour-Browne, but had again disappeared the following year. *Limnocythere mirabilis* is claimed by Zschokke as a member of the deep-water fauna of the Swiss lakes, which is of northern origin and finds only in deep waters the conditions necessary for existence in its southern station. But in 1905 I found this species in a shallow rain-pool near Biskra in Algeria, and another species, *L. incisa*, in a stream which irrigates the Oasis of Oumach.

#### *The Plankton of Ennerdale Water.*

The discovery of *Limnocalanus macrurus* in Ennerdale indicated at least a possibility that other "relict" Crustacea might be found there, and made it most desirable that the lake should be carefully explored. With this purpose in view I visited the lake at the end of September 1922, and made special efforts to collect the Crustacea of the deep water. The lake is shallow at its western end, but the eastern part is a deep narrow trough with a maximum depth of 148 feet. The shores are rocky, and with a very steep slope.

The weather during my stay was unfavourable, but I was able to search a large part of the deep trough with a coarse tow-net and light dredge, and also to take plankton samples on three successive nights. Neither *Mysis relicta* nor any Amphipods were taken. This negative result should be tested by examination of the stomachs of Char (*Salmo alpinus*), but I have not been able to obtain specimens.

Table 4 gives the composition of the plankton between September 27th and 29th. It is of course impossible to obtain accurate information as to the vertical distribution of plankton without the use of a closing net and a succession of short vertical hauls, but I do not think that such accuracy is, in general, necessary, and a fair approximation to the truth may be got with less effort and simpler means. My own collections were made with an ordinary small plankton net, which was let down, together with a weight, to the required depth and then towed a distance of about 100 yards. Naturally the net fished both going down and coming up, but the results of the different hauls are so distinct that they do in my opinion give information as to the vertical distribution. I have not attempted to compare different hauls by absolute numbers, but have counted the individuals of each species in the whole or in part of the collection, and expressed their frequency as percentages of the whole number of individuals of all species counted. This method gives an accurate statement of the comparative frequency, though not of the absolute numbers of any species, and it admits of a comparison being made between samples from the same or different lakes however they may have been taken. Similar figures are given for Wastwater and Coniston for purposes of comparison.

TABLE 4.—Composition of the Plankton of Ennerdale, Wastwater, and Coniston.

The figures give numbers of individuals of each species per cent. of whole number counted.

ENNERDALE WATER. Sept. 27-30, 1922.	Surface.		At Night—Surface.				Deep Water.			
	Over Medium Depth.	Over Deep Water.	Medium Depth.	Shallow Water.	Medium & Deep Water.	Shallow Water.				
	1	2	3	4	5	6	7	8	9	10
<i>Sida crystallina</i> .....	—	—	4.2	.37	2.3	—	—	—	—	—
<i>Holopedium gibberum</i> .....	.7	—	20.2	26.1	32.1	33.6	12.6	19.6	5.6	3.6
<i>Bythotrephes longimanus</i> .....	3.4	.78	1.5	10.4	1.15	17.2	6.4	.89	4.67	7.2
<i>Bosmina obtusirostris</i> .....	—	—	—	—	—	—	.7	—	—	1.2
<i>Diaptomus gracilis</i> .....	69.4	7.8	16.2	49.2	16	28.1	46.8	46.4	34.6	50.8
<i>Limnocalanus macrurus</i> .....	23.8	81.3	58.2	13	47.1	19	33.4	33	54.3	36.9

WASTWATER. Oct. 1, 1922.	Surface.	80 feet.	100 feet.	120 feet.
<i>Bosmina obtusirostris</i> .....	52.5	40	40.2	48.6
<i>Bythotrephes longimanus</i> .....	7.05	4.2	5.88	9.6
<i>Leptodora kindti</i> .....	.64	.52	.98	2.05
<i>Diaptomus gracilis</i> .....	21.7	25.2	28.4	27.4
<i>Cyclops abyssorum</i> .....	17.9	30	24.5	12.3

CONISTON. Oct. 2, 1922.	Surface. Fine-Net.	Surface. Coarse Net.	50-80 feet.	Below 100 feet.
<i>Daphnia galeata</i> .....	4.9	37.2	57.7	48.9
<i>Bythotrephes longimanus</i> .....	+	1.4	1.86	2.5
<i>Leptodora kindti</i> .....	+	—	5.6	3.9
<i>Diaptomus gracilis</i> .....	93	47.2	21	28.1
<i>Cyclops abyssorum</i> .....	2.09	14	11.4	16.4

It is clear from the table that the plankton is by no means uniform throughout the lake either vertically or horizontally, neither is it the same by night and by day.

The chief component of the plankton is *Diaptomus gracilis*, which is distributed throughout the lake, but is relatively more abundant in the western end than in the deep eastern trough, and has a distinct preference for the surface. The figures given for the deep-water samples must be discounted to some extent, owing to the fishing of the net going down and coming up. It is curious that this species seemed to be present in absolutely smaller numbers on the surface by night than by day.

*Limnocalanus* is also distributed all over the lake, but is found only in small numbers in the shallow water. It abounds both on the surface and in deep water in the eastern trough, and may greatly exceed *D. gracilis* in numbers. Although common at all times on the surface, it is noticeably more abundant during darkness.

*Holopedium gibberum* is only exceptionally found on the surface by day, but is common in deep water, and at night forms a large part of the surface plankton.

*Bosmina obtusirostris*, though apparently fairly common at some seasons, was almost absent from the lake at the time of my visit, the few specimens taken being in deep-water samples.

A curious feature of the plankton was the appearance of *Sida crystallina* on the surface at night. It was not taken during the day in any collections in open water, but occurred in three out of four plankton samples taken at night. All these samples were taken at the surface over water 80-120 feet deep, the only sample in which *Sida* was not found having been taken in shallow water. The specimens taken were almost all males.

#### THE ENTOMOSTRACA OF THE TARNs.

The occurrence of *Diaptomus laticeps* in Hawes Water and in Goats Water (as recorded by Brady) raised the expectation that the fauna of the high tarns of the district might prove to include other species representative of the arctic-alpine Entomostraca which do not occur in the lakes, and, at the end of September 1922, I visited some of these tarns and made collections in them and in pools and bogs up to an elevation of about 2000 feet. The result did not fulfil expectation, since *D. laticeps* was not found in any tarn other than Goats Water. There was also a notable absence of the northern forms of Harpacticid, with the exception of *Canthocamptus cuspidatus*, which seems to be comparatively common in *Sphagnum* in running water where the temperature is low. Nevertheless I think the results are of sufficient interest to be given in some detail. The complete list of species is shown in tabular form.

1. *Floutern Tarn*. This tarn, which is fairly deep and contains trout, lies, at a height of about 1250 feet, just on the east of the watershed between Ennerdale and Crummock valleys, in a deep hollow in the grassy moor. It is on the edge of the area of the Skiddaw Slates, the granite hill of Great Borne rising steeply on the south. All around the tarn is swampy ground, with trickling springs and hollows filled with *Sphagnum*.

The water is dark and peaty, and the marginal vegetation consists of *Littorella* (dominant) and *Lobelia*. The tarn drains into Crummock. Seven species only of Entomostraca were taken, *Bosmina obtusirostris* being the dominant species. A large proportion of the females were ehippial, but only one male was seen. Very few females carried summer eggs, so that the colony was probably at its maximum and about to die out. *Diaptomus gracilis* was abundant, a large proportion being males. All were of a striking blue colour, but of quite typical structure.

2. *Greendale Tarn* lies, at a height of 1320 feet, on the Borrowdale volcanic series at the head of a glen north of Wastwater. West of it is a gently sloping moor, while east of it rises the bare rocky Middle Fell. The tarn is very shallow, with clear water and stony bottom, the vegetation consisting of *Lobelia*, *Littorella*, *Callitriche*, *Myriophyllum*, and *Isotetes*. While I was unfortunately unable to take the temperature, I can say that the water was (Oct. 1st, 1922) so intensely cold that it was impossible to wade out and collect in the open. Eleven species of Entomostraca were taken, among which *Diaphanosoma brachyurum* was the most abundant. *Bosmina* was common, but none were ehippial. *Diaptomus gracilis* was abundant, and here of a fine red colour\*, but the majority were immature. *Alonopsis elongata* was abundant, but none were sexual.

3. *Lerers Water*, altitude 1350 feet, lies on the Borrowdale volcanic series, and is a rather large, nearly circular, tarn in a barren rocky corrie. It owes its existence to a morainic dam, but its outlet is artificially controlled and its level somewhat raised for the supply of water to the Coniston copper works. The floor and sides of the tarn are rocky and without any vegetation, and Entomostraca are almost absent. The only species found in quantity was *Alonopsis elongata*, and, besides this species, only a single individual each of *Bosmina obtusirostris* and *Acroperus harpe* were taken in spite of prolonged search. On the other hand, *B. obtusirostris* was found common in quite a small pool near the tarn.

The lifelessness of this tarn is rather remarkable, and I can offer no explanation.

4. *Low Water*, at a height of 1786 feet, lies in a circular corrie beneath the crags of Coniston Old Man, and is, as Levers Water, partly dammed for

\* Ward (1904) notes specially the red colour of copepods in elevated lakes.



the service of the mines. It also is rocky, deep, and without vegetation, the water rather dark coloured. The fauna consisted of four species only, and these in small numbers. *Diaptomus gracilis* was here of a rich red-orange colour. A curious feature of the fauna was the extreme blackness of the *Alonopsis elongata*, which proved to be due to the retention of the old shell at moulting. The majority of the individuals showed three old shell valves adhering and forming "lines of growth." In other tarns and in the lakes similar individuals were occasionally seen, but the feature was pronounced only in Low Water. Lilljeborg mentions the same thing as characteristic of specimens of this species from the high north of Sweden, and it is apparently a character connected in some way with the low temperature of the habitat.

5. *Goats Water*, 1646 feet, is a small tarn in acombe on the north-east side of Coniston Old Man. It owes its existence to a dam of rocks fallen from Dow Crag, and the water from it soaks through the dam and issues as a stream some distance below. The water is deep and clear, the shore rocky and entirely barren. The fauna was found to be very scanty, but six species were taken, the most noticeable being *Diaptomus laticeps*, conspicuous from its red colour.

6. *Highlow Tarn*, about 2 miles N.E. of Coniston, at a height of about 600 feet, is mainly of artificial origin, being due to the union of several small shallow tarns by the damming of the stream. Lying comparatively low, with shelving banks, its vegetation is rich and includes *Nymphæa*. Consequently its fauna is quite different from that of high tarns. *Ceriodaphnia*, *Polyphemus*, and *Bosmina longirostris* are common, and *Volvox* was present in such quantity as to give the water a thick green colour.

#### 7. *Sphagnum pools and spring waters.*

On the high ground of the Floutern Pass and round the foot of Coniston Old Man there is much swampy ground, often with little rills of running water, and occasional pools largely filled with *Sphagnum*. The water was uniformly very cold.

By the outflow of Greendale Tarn there are a number of small pools generally margined with *Sphagnum*, but one of them, which was of some depth, was choked with *Callitriche* and contained some larvæ of the Newt *Molge cristatus*. These larvæ were kindly identified for me by Miss J. B. Procter, who informs me that they were either newly hatched or only a few days old. This very late hatching is very unusual, and no doubt due to the coldness of the water.

The *Sphagnum* in running water was commonly tenanted by *Canthocamptus cuspidatus*, a slow-moving pink-coloured Harpacticoid which is a characteristic northern species. In pools and springs the moss contained either *C. cuspidatus*, *C. zschokkei*, or *C. pygmaeus*, but never more than one species in one

place. Several species of *Cyclops* were taken, of which the most interesting is *C. venustus*, which was common in pools on Floutern Pass and was also found by Greendale Tarn. It was somewhat unexpected to find *C. nanus* in pools on Floutern Pass since I regard this species as a warm-water form.

It is worth noticing that *Acantholeberis curvirostris* was only found in two high-lying pools. This is a species found in lime-free bog waters, but it is evidently not a cold-water northern form. *Alona rustica* and *Chydorus piger* are species of similar preference, and were found rather infrequently on the high ground.

TABLE 5.—The Crustacea of the Tarns.

	Highlow Tarn.	Floutern Tarn.	Greendale Tarn.	Levers Water.	Low Water.	Goats Water.
<i>Diaphanosoma brachyurum</i> .....	+	+	+			
<i>Ceriodaphnia pulchella</i> .....	+					
<i>Dosmina longirostris</i> .....	+					
„ <i>obtusirostris</i> .....	..	+	+	+	..	+
<i>Eurycerus lamellatus</i> .....	..	..	+			
<i>Acroporus harpæ</i> .....	..	+	..	+	..	+
<i>Alonopsis elongata</i> .....	..	+	+	+	+	+
<i>Alona affinis</i> .....	..	..	+			
<i>Alonella nana</i> .....	..	+				
„ <i>excisa</i> .....	..	..	+			
<i>Graptoleberis testudinaria</i> .....	..	..	+			
<i>Polyphemus pediculus</i> .....	+					
<i>Cyclops leuckarti</i> .....	+					
„ <i>agilis</i> .....	+	+	+	..	+	+
„ <i>viridis</i> .....	..	..	+	..	+	
„ <i>fuscus</i> .....	..	..	+			
<i>Diaptomus gracilis</i> .....	+	+	+	..	+	
„ <i>laticeps</i> .....	..	..	..	..	..	+
<i>Canthocamptus zachvatkini</i> .....	..	..	..	..	..	+

Highlow Tarn has all the characters of a lowland pool, but the remaining tarns described are probably fairly representative of all the high-lying waters of the district. Those examined fall into two groups, of the peaty and the rocky type, the former represented by Floutern and Greendale Tarns and the latter by Levers Water, Low Water, and Goats Water. Floutern and Greendale Tarns have a relatively rich Entomostracan fauna characterized

by *Diaphanosoma*, while the rocky tarns of Coniston have a very scanty fauna, both of species and individuals. The brilliant colour, either red or blue, of *D. gracilis* in these high tarns is very striking.

The means of dispersal of the species is a problem of some obscurity. All the tarns are of comparatively recent origin, owing their existence to morainic dams or rock-falls, and each, as a rule, occupies the head of a lateral valley.

Keilhack, studying high-lying waters in the Dauphiné Alps, concluded that distribution of species was effected by migratory birds, and that watersheds rarely, if ever, exert any influence on distribution. While it is impossible to offer any other satisfactory explanation, the agency of birds, especially in the Lakeland area, seems to be of doubtful efficacy. A detailed survey of the tarns of this compact and uniform district, with special reference to the dissemination of species, would probably lead to results of great general interest.

*Notes on some of the Species.*

*LIMNOCALANUS MACRURUS, Sars.*

The occurrence of this fine Centropagid in Ennerdale is rather a startling discovery, and raises problems of exceptional interest. It was first recognized in a collection made by Dr. Pearsall on Sept. 23, 1921, the sample containing five specimens. As a result of this discovery Dr. Pearsall arranged for a series of collections to be made in the lake, and I also visited it myself on Sept. 27, 1922, but, although I am able to give some account of its distribution in the lake and its seasonal cycle, the facts are by no means complete, and can only be ascertained by quantitative methods with suitable apparatus. So far as information goes at present, the species is very abundant in the lake and occurs in every part of it, at all events in autumn, which is the period of maximum development; but it is far more abundant in the deep eastern trough, and occurs only in small numbers in the shallow western end. All previous observations, by Ekman and others, agree in showing that *L. macrurus* is only exceptionally found at the surface, and is almost entirely confined to water below a depth of 5 metres. Further, the maximum temperature of water in which it lives is 14° C., but even when the temperature is lower than this it does not come to the surface. In Ennerdale this is not the case. The first collection in which it occurred was made on the surface (in stormy weather it is true), the temperature of the water being 14.4° C., and my own collections between Sept. 27 and 29 proved that it lived at that time in considerable numbers at the surface, although it certainly was more abundant in deeper water, down to about 80 feet. It is impossible to give exact figures, since I had no closing net at my disposal, but the figures given in Table 2 (p. 417) will serve to show the distribution at that time with, I believe, a sufficient approximation to the truth. I was unfortunately unable to take temperature observations.

Diurnal migration of the species was strongly marked at the time of my visit. On three successive nights surface plankton samples were taken over the shallow and medium (50–70 feet) depths, and in each case *Limnocalanus* was found in much greater numbers than during the day. The figures in the table do not bring out this fact so clearly as would have been the case if absolute numbers could have been given, but the difference between day and night plankton was quite obvious and striking on the spot.

So far as concerns seasonal distribution, the facts with regard to *Limnocalanus* in Ennerdale are somewhat uncertain. Ekman has shown that in the Baltic lakes there is only one breeding-period—in autumn. Young appear first in March, and by May the first-hatched young are fully grown. But there is then a period of about five months during which little or no growth takes place and the genital organs remained undeveloped. Sexual maturity is reached in autumn, and breeding begins in November at a temperature of about 7° C. The adults of the previous year die off in spring and all have disappeared by May.

Dr. Pearsall's collections may be regarded as indicating a similar life-cycle in Ennerdale, but are by no means conclusive. Neither young nor adult were taken on Feb. 18, 1922, but two adults and many young were found in a sample from the shallow end of the lake on April 20, though, curiously enough, none at all were taken in a deep-water collection on the same day. In June and July no young, but a very few adults, were taken; but in October adults were common in 60 feet of water. It seems safe to say that young are only found in spring, and that adults are abundant, and even the commonest plankton species, in September and October.

The interest of this species lies more, however, in its geographical distribution and its origin as a member of the fresh-water fauna, and it is necessary to go into this question in some detail since its occurrence in Ennerdale raises a particular difficult geological problem.

Ekman has dealt exhaustively with the structure and distribution of *L. macrurus* (1913), particularly with reference to the Baltic area, and his results may be summarized as follows:—

1. *L. macrurus* of fresh-water lakes is not specifically separable from *L. grimaldii*, which inhabits brackish water in the Baltic and Caspian Seas and along the coasts of Alaska and Siberia.

The differences are:—

- (a) Shape of head, the dorsal contour being more swollen in *L. macrurus*.
- (b) In *L. grimaldii* the last thoracic segment is rather triangular or pointed, or may have a minute hook-like projection, whereas it is rounded in *L. macrurus*.
- (c) The antennæ are longer in *L. grimaldii*.
- (d) The furcal rami of *L. grimaldii* are longer than in *L. macrurus*.

While the two extremes are readily distinguished, they are united by local varieties presenting every intermediate condition.

2. In Europe *L. macrurus* is only found in lakes which can be proved to have been separated from the sea in post-Glacial times. It is therefore a "relict" form in the strictest sense. It has not arrived in any of the lakes it now inhabits by active migration.

3. The shape of the head in *L. macrurus*, while not at all variable among individuals in any given lake, varies greatly according to the locality, and it can be shown that those lakes (in Europe) which contain the extreme fresh-water form have been separated longest from the sea, whilst in more recent lakes the *Limnocalanus* approaches more nearly to the *grimaldi* form.

4. It is evident that *L. grimaldii* is the parent form, and that *L. macrurus* is a variant from it which has arisen independently in many places, the effect of the change of medium being always in the same direction.

5. The first step in the transformation occurred in the Baltic during the "Ancylus Lake" period, and the Baltic lakes in which *Limnocalanus* occurs are relicts of the Ancylus lake.

With the most interesting speculations of Ekman on the subject of the origin of species founded on these facts we have no concern here.

Now, while it seems to me that Ekman's conclusions with regard to the *Limnocalanus* of the Baltic area and of the Caspian Sea are entirely well founded, there are certain criticisms to be made, and it is difficult to extend his explanation to the *Limnocalanus* of Ennerdale and the lakes of North America in which it occurs.

In the first place I cannot unreservedly accept Ekman's basis of measurement of the head form on which much of his argument depends. Ekman has adopted the following system of measurement:—

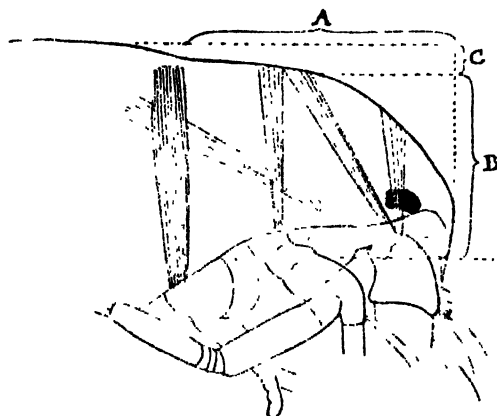
- (1) Head-length—to the dorsal groove immediately in front of the mandibular muscle. (See text-fig. 2.)
- (2) Head-height—B—expressed as a percentage of half the head-length.
- (3) Height of vertex above or below the dorsal line of the thorax expressed as a percentage of half the head-length.

The last measurement is negative in all the *grimaldii* forms, and positive only in the extreme *macrurus* forms where the dorsal contour of the head swells up above the dorsal line of the thorax.

While the first and second measurements are fairly definite and extraordinarily constant, the third seems to me so uncertain as to be of little value, since (as Ekman has himself pointed out) the selection of a dorsal horizontal base-line is a matter of guess-work. I have been quite unable to find agreement between his own figures for this character and the drawings of the specimens from which the measurements were taken; in fact, these measurements cannot, as I believe, give a real definition of the shape of the head, which can only be shown in a drawing. Still, for purposes of comparison, I give, in Table 6, measurements taken by Ekman's methods for the Ennerdale and other forms.

It is evident that, if *L. grimaldii* be the parent form, those races which approach it most nearly in shape of head and in other respects may be regarded as most nearly related, and consequently more recently separated from it. It is therefore of some interest to apply Ekman's system of measurement to races other than those of the Baltic region, and to see if by that means any clue to their age may be found.

FIG. 2.



*Limnocalanus macrurus* from Ennerdale, showing method of measurement.

A. Head-length. B. Head-height. C. Crown-level.

TABLE 6.—Measurements of *Limnocalanus macrurus* and *L. grimaldii*.

Figures marked \* are taken from Ekman, 1914.

		Length.	Fucal rami. Per cent. of body.	Head- length. A.	Head- height. B.	Crown- level.	A & B.
Ennerdale .....	♀	2.18	13.1	.29	157	-26	131
	♂	2.06	14				
Sweden—Mälaren .....	♀	2.34	16	.32	126	-16	110
	♂	2.3	16				
„ Insjön .....	♀	2.1	15.7	.33	137	+4.4	141.4
U.S.A.—Green Lake ....	♀	2.28	14	.32	134	-11.5	122.5
	♂	2.24	13.8				
„ Lake Erie .....	♀	2.86	13.3	.37	140	-17	123
	♂	2.7	13.3				
„ Lake Canandaigua	♀	2.53	15	.37	135	-16	119
	♂	2.51	15	.35	141	-13	128
Caspian Sea .....	♀	2.59	15.8	—	90*	-25*	65*

I possess a few specimens of *L. grimaldii* from the Caspian Sea which were given to me by the late Canon Norman some years ago, and by the kindness of Dr. C. Juday I have had the opportunity of examining *L. macrurus* from Green Lake, Lake Erie, and Lake Canandaigua (one of the Finger Lakes east of Lake Ontario). Dr. S. Ekman also has been good enough to send me specimens from Lakes Mälaren and Insjön in Sweden.

Measurements of these races are given in Table 6.

So far as the numerical expression of the head-form goes, the Ennerdale race cannot be compared with any of the Baltic races, since in none of them is so great a head-height accompanied by so low a crown-level. The only race with similar head-height (Lake Mjösen) has a dorsal swelling rising above the horizontal dorsal line. On the other hand, the high, evenly-rounded dorsal outline rather closely resembles Ekman's figure of the race from Unden in Sweden, though that race has a crown-height according to his measurements of only - 6. It seems that in respect of this character the Ennerdale race stands somewhat apart, but that it must have been evolved from the *grimaldii*-type at a comparatively remote period.

The North American races differ but little in head-form, and conform more closely to the Baltic type. Both have a posterior more or less horizontal part with an anterior descending slope, and agree very closely in appearance with the Mälaren form, though the measurements do not agree very well with those given for that race (Pl. 23. fig. 6). But, as compared with the Ennerdale race (Pl. 23. fig. 1), specimens from North America certainly approach far more nearly to the *grimaldii* type, and are consequently to be regarded as of more recent origin.

This conclusion is strengthened by a consideration of the other characters in which the two forms differ.

(1) The true *grimaldii* form of the Arctic Ocean (examples from Jana River) measure over 3 mm., while the somewhat modified form of the Baltic may also attain 3 mm. (Gulf of Finland). It is, on the other hand, roughly true of the Baltic area that the oldest fresh-water races are the smallest (Sommen 1.87 mm., Unden 1.72 mm.). Small size is therefore to some extent evidence of prolonged sojourn in fresh water. In respect of this character the Ennerdale race (2.18 mm.) holds a more or less middle position. The race from Lake Erie, on the other hand, is one of the largest known (2.86 mm.), greatly exceeding any other fresh-water race and exceeded only by those of North Siberia and the Gulf of Finland in salt water. The Green Lake form, though similar in structure, is but little larger than that of the Ennerdale race.

(2) The antenna in the true *grimaldii* form reaches to the base of the furca or even further (Pl. 23. fig. 5), whereas in typical *L. macrurus* it does not extend further than the first abdominal segment. In this respect the Ennerdale race belongs to the extreme fresh-water type, while those from North

America have the antennæ slightly longer. In the Mälaren race, which is one of the most primitive forms, the antennæ in the female may reach to the base of the furca.

(3) The length of the furcal rami in proportion to the whole body differs in different lakes, but the published information on this point is too scanty to admit of a definite conclusion as to whether there is any connection between the shortness of the furca and the length of sojourn in fresh water. The furcal rami of the Ennerdale and the American forms are notably shorter than those of the *grimaldii* form from the Caspian, but, on the other hand, both the Mälaren and the Insjön races have these rami as long as or longer than those of my Caspian specimens.

(4) The pointed triangular form of the lateral expansion of the last thoracic segment has been given by Prof. Sars as one of the distinctive characters of *L. grimaldii*, since in all the fresh-water races this segment is simply rounded. I find in my Caspian Sea specimens that this segment is produced laterally into a very well-defined point (Pl. 23. fig. 5), and it is important to note that a similar point is to be found in some of the specimens from Green Lake and from Lake Canandaigua, and very rarely also in those from Lake Erie, while the Ennerdale race has the segment simply rounded. This character, small as it may appear, seems to be of importance in indicating relationship with the parent form, and the North American race must for this reason also be regarded as of comparatively recent origin. The primitive Mälaren race has this segment generally very slightly angular, and occasionally there is a definite point as in *L. grimaldii* (Pl. 23. fig. 8).

It is remarkable that, in spite of the considerable differences in general body-form between the brackish and fresh-water races of *Limnocalanus*, there is no appreciable difference to be found between any of the appendages of the two forms, except as regards the length of the antennules. I have compared the appendages of the seven races available to me, and find the agreement perfect in almost every detail. There is, however, one very slight difference which may be peculiar to the Caspian race, namely the absence of a spine on the outer distal angle of the first joint of the exopodite in the right fifth foot of the male. Prof. Sars does not figure a spine in this position, neither was it present in a specimen examined by me, but it is present in all other races of which figures are published.

Having dealt, so far as I am able, with the biology and structure of the Ennerdale and North American races of *Limnocalanus* in comparison with others, there remains the consideration of the question as to whether these races can be regarded as "relicts" in the same sense as those of the Baltic area.

It must be admitted that in neither case can any definite answer be given.

There can be little doubt that the whole of the Lakeland area was completely covered by ice during the Glacial period, though the view that



the lakes themselves are glacially-eroded rock-basins is not universally admitted. In any case, however, the fauna must have reached these lakes after the withdrawal of the ice.

According to Clifton Ward (1876) the passing of the Glacial period was immediately followed by a submergence of the whole district by as much as 2000 feet, which would leave only the highest ground projecting as a number of small islands in the midst of an arctic sea. If a submergence to this or to a much smaller extent can be admitted, then *L. macrurus* might well be a relict of this sea left in Ennerdale. Unfortunately Ward's conclusions are not admitted by geologists of the present day, though I have not been able to find in any literature available to me any serious discussion of the question of post-Glacial changes of level in this district. The matter is hardly referred to in Marr's 'Geology of the Lake District,' but apparently he does not admit a submergence of more than a few feet, which could not have made any material difference to the distribution of land and sea.

If a submergence to an extent sufficient to bring the sea in the first instance into direct connection with the Ennerdale basin cannot be conceded, there are only two alternatives. Either the interpretation of the geological facts is wrong, or a marine species has either been able to migrate for miles up a rushing stream of fresh water or has been transported directly into the lake. No biologist would for a moment consider such migration or transference to be even conceivable. It must be remembered that we are dealing with a species which occurs in this one lake only in the British Isles and cannot have been transported to its present habitat from any other lake in Britain.

Even if Clifton Ward's great submergence could be proved true, it is still a little doubtful if it would satisfactorily explain the facts. Our knowledge of marine relicts seems to point to the conclusion that transformation of marine species into fresh-water relicts has rarely happened, and only in cases where very large areas of water have been involved. Thus the *L. macrurus* of the Baltic area owe their origin to the transformation of the Yoldia Sea into the Ancylus Lake, rather than to the separation of lakes from the Yoldia Sea itself. In other words, *L. grimaldii* was transformed into a form of *L. macrurus* in the Ancylus Lake and not, in the first instance, in the existing inland lakes. Similarly, we should not expect that a race of *L. grimaldii* could have survived in so small a lake as Ennerdale itself even if it could be shown that the lake had itself been cut off from the sea.

To explain the occurrence of this species in Ennerdale in the same way as its occurrence in the Baltic lakes, it is more reasonable to assume that the Irish Sea itself has passed through a history somewhat similar to that of the Baltic, having been changed from an arctic sea containing *L. grimaldii* to a fresh or brackish water, and finally to its present condition, and that during the second phase *L. grimaldii* became in part transformed in the direction of *L. macrurus*. Further, that conditions were such that, on the renewed

entrance of salt water, immigration into Ennerdale was possible. I must freely admit that such a supposition is not supported by the geological evidence, but it does not appear to me to be an altogether impossible assumption in view of the following facts.

There is evidence of a subsidence of land immediately after the withdrawal of the ice, and of a later elevation at a time when the submerged peat-beds and forests were formed. But the amount of the latter elevation is uncertain, and there is no positive evidence of a rise of more than 60 feet. On the other hand, the occurrence in Ireland of the Red Deer and Reindeer seem to necessitate the supposition that there was some land connection between England and Ireland in neolithic time, and, as Jukes-Browne has pointed out, firstly it is possible that this elevation may have been greater than has been supposed, and secondly it is very probable that the floor of the Irish Sea, which was thickly covered by drift, has been greatly eroded and re-modelled. It may consequently have been at so much higher a level that a comparatively small elevation may have sufficed to effect a land connection with partial or complete damming off of the sea.

Dr. Scharff has assumed the existence of a great lake occupying the trough of the Irish Sea to explain the present distribution of the genus *Coregonus* in Britain and Ireland, and if such a lake could have originated by freshening of a Glacial sea, not only might *L. grimaldii* have been therein isolated and transformed, but also *Mysis oculata* could in this way have been changed into *M. relicta* and have reached its present station in Lough Neagh.

There are two obvious objections, namely that *M. relicta* does not live in Ennerdale and *L. macrurus* does not occur in Lough Neagh. Further, that conditions which would allow the latter to reach Ennerdale should also allow it to reach Wastwater and perhaps other lakes. To these objections not much importance need be attached until more is known of the conditions which determine the distribution of fresh-water Crustacea. Not only does the plankton of Lough Neagh differ radically from that of the English lakes in general, but these lakes differ unaccountably among themselves, and Wastwater and Ennerdale, alike as they seem to be in physical conditions, contain quite different plankton. Hence it cannot be assumed that a species would establish itself in every lake to which it had access.

It is equally difficult to explain the distribution of *Limnocalanus* in North America. Its distribution follows rather closely that of *Mysis relicta*, as shown in Table 7, page 434.

*L. macrurus* therefore occurs in all the great lakes and in a number of lakes belonging to the same drainage system, but not, so far as I can find, in any lakes outside this region.

So far as the origin of these species is concerned, the view once held that the Great Lakes were themselves at one time invaded by the sea and that *M. relicta* is a true relict within them has been generally abandoned, but at the same time there appears to be no doubt that the sea did, at a late stage

in the post-Glacial history of the region, penetrate up the St. Lawrence valley and flood the basins of Lake Ontario and of Lake Champlain. At this time there existed an eastern outlet from Lake Huron through the Ottawa valley. The marine deposits of this stage are found at a height of 400-500 feet by Lake Champlain and at 600 feet near the east end of Lake Ontario. It would appear that we have here all the conditions necessary for the isolation and modification of these two "relict" species, but there are

TABLE 7.

	<i>Mysis</i> <i>relicta</i> .	<i>Limnocalanus</i> <i>macrurus</i> .
Lake Ontario* . . . .	+	+
" Michigan . . . .	+	+
" Superior . . . .	+	+
" Huron . . . . .	-	+
" St. Clair . . . . .	-	+
" Erie . . . . .	+	+
" Geneva . . . . .	+	+
Green Lake . . . . .	+	+
The Finger Lakes:—		
Canandaigua . . . .	+	+
Cayuga . . . . .	+	+
Keuka . . . . .	+	
Owasco . . . . .	-	+
Seneca . . . . .	+	+
Skanateles . . . .	-	+

two great difficulties in the way, namely the absence of *Mysis relicta* from Lakes Ontario and Champlain and the existence at or before that time of the Niagara Falls, which would be an effective bar to migration into the other lakes. On the other hand, the absence of a species from a lake at the present day does not necessarily prove that it has never existed there, and the occurrence of both species in the Finger Lakes, which form part of the drainage system of Ontario, seems to be good evidence that they have reached these lakes from Ontario. Their penetration into the other Great Lakes must, one must suppose, have taken place by way of the Ottawa connection, and in any case we are forced to assume for *L. macrurus* a capacity for active migration up rivers which is denied by Ekman.

\* So far as I know, there is no published record of the occurrence of *Limnocalanus* in Lake Ontario, but Dr. C. Juday informs me that he has found it in a plankton sample from this lake taken by Dr. N. A. Clement in October 1922. I am greatly indebted to Dr. Juday for this information.

The recent discovery of another species of the genus (*L. johanseni*, Marsh) in a tundra pool in Alaska seems to raise a new problem altogether. But Marsh's description is very short, and it is not clear that this new species is really distinct from *L. grimaldii* or *L. macrurus*, the only essential difference mentioned being the shortness of the furcal rami. It is important that this species should be fully described and its distribution ascertained.

**DIAPTOMUS LATICEPS, Sars.**

Syn. *D. hircus*, Brady.

Brady's species, *D. hircus*, was established in 1891 on specimens taken from Goats Water, an elevated tarn on the slopes of Coniston Old Man. There can be no doubt that his species is identical with *D. laticeps*, from which it differs in no essential character.

It is an arctic and alpine species occurring mainly in Scandinavia, but recorded from Akmolinsk in Russia, the Julian Alps, Serbia, and Herzegovina. It has also been taken in several lakes in Scotland and in Ireland.

The only lake in the Lake District in which the species is found is Hawes Water, which is the highest of all (694 feet), and for that reason may have a different temperature. It seemed likely that *D. laticeps* might be common in the high tarns of the district, but, as I have said in my notes on these tarns, this is not the case. On the other hand, our knowledge of the fauna of these tarns is very incomplete, and it may prove to occur in the tarns of Harter Fell and to have reached Hawes Water from thence.

**CYCLOPS ABYSSORUM, Sars.**

This species has been found in all the lakes examined with the exception of Ennerdale, Derwentwater, Bassenthwaite, and Esthwaite. In Ennerdale no limnetic species of *Cyclops* was seen in any of the samples taken either by Dr. Pearsall or myself, but Brady has recorded the occurrence there of *C. ricinus*. The occurrence of that species in the plankton of this district seems most unlikely, and it is more probable that Brady had specimens of *C. abyssorum*, in which case the species once inhabited Ennerdale but has now disappeared.

Prof. Brady has recorded the occurrence of this species in Windermere and Coniston in deep water in Aug. 1883, and Prof. Sars, in his 'Crustacea of Norway,' describes it as inhabiting only the deeper layers of water. My own collections in Wastwater and Coniston show that, though it is found in autumn on the surface, it is distinctly more abundant in deeper water, and its absence from Derwentwater, Bassenthwaite, and Esthwaite is no doubt largely due to their small depth. It is replaced in these lakes by *C. leuckarti*. In 1911 a few specimens were taken by me in Bassenthwaite, but it is evidently not an established member of the plankton in that lake.

The seasonal cycle of the species cannot be determined with certainty from Dr. Pearsall's collections, which were mostly taken on the surface, and therefore are unreliable in the case of a deep-water species; but a careful comparison of the records from the different lakes leads to the conclusion that there is only one period of breeding, namely in the autumn, and that the adults die after breeding, the species passing the winter either in the form of resting-eggs or as nauplii. In all the lakes mature specimens were rare or absent in spring and early summer, but were abundant in collections made between August and November. Females bearing eggs were found in Hawes Water in August, but in the other lakes only in September or October. If this is a true statement of the breeding cycle, it resembles very closely the cycle in *L. macrurus*—another cold-water northern form. On the

TABLE 8.—Measurements of *Cyclops abyssorum*.

	Length (including furca).	Furca. Per cent. of body.	Furcal Setæ.				Seta 3. Per cent. of body.
			Outer- most.	2	3	4	
Wastwater .....	1.35 mm.	13.3	100	418	481	194	34.4
Crummock .....	1.43	13.8	"	402	484	186	35.3
Coniston .....	1.44	13.7	"	394	485	190	36.3
Ullawater .....	1.42	11.6	"	388	456	190	33
Hawes Water ....	1.45	12.8	"	329	379	250	31
Windermere .....	1.77	11.8	"	346	423	169	31
Grasmere .....	1.68	14.9	"	341	424	190	32.5

other hand, Scheffelt (1908) and Burckhardt (1900) found two breeding-periods in the *Cyclops* of the *strenuus*-group studied by them in the Black Forest and Swiss Lakes respectively. It is not, however, clear with what race or species these authors were dealing, since the species of this group recognized by Sars and Lilljeborg as distinct have not been generally admitted, and many writers have followed Schmeil in including all within the species *C. strenuus*. It seems certain that the three species *C. lacustris*, *C. scutifer*, and *C. vicinus* should be maintained. Whether *C. abyssorum* is sufficiently distinct from *C. strenuus* as defined by Sars is rather more uncertain, but the evidence goes to show that it is a limnetic and cold-water representative of *C. strenuus*, which it is convenient to distinguish. It is readily distinguished from typical *C. strenuus* by the greater length of the antennæ, of the furcal rami, and of the furcal setæ. The much greater

relative length of the innermost seta in *C. abyssorum* is perhaps the easiest character by which the species may be separated, but Prof. Sars has enumerated a number of details wherein the species differ. It is to be hoped that Prof. Sars' limitation of these species will be followed, since it is most probable that they will be found to have different life-cycles and different habitats and distribution. The general adoption of Schmeil's definition of *C. strenuus* has made comparison of statements with regard to these questions unreliable and indeed valueless. So far as published information goes, it seems that *C. abyssorum* is confined to northern lakes, and is absent from Swiss lakes, where apparently a form resembling *C. scutifer* takes its place.

The Lake District species is undoubtedly *C. abyssorum*, though the form of the receptaculum differs to some extent from Prof. Sars' description and agrees more closely with that of *C. lacustris*.

Those who (*e.g.* Graeter, 1903) accept the species *C. strenuus* in its wider sense lay great stress on its variability, and it might be supposed, if their view is correct, that great differences would be found between individuals from different lakes. This is far from being the case. In general form of body—particularly in the expansion of the last thoracic segment—there is, so far as I can find, no appreciable variation. In size, in the length of the furca and the relative length of the furcal setae there are differences, but they are not great. In Table 8 I have given measurements of individuals from seven of the lakes. These are, in the case of the first four, averages from ten specimens, but in the remainder of from two to six.

It will be seen that the smallest specimens are from Wastwater and the largest from Windermere and Grasmere, which is hardly according to expectation. Those from the "primitive" lakes agree in having the longest setae, together with rather long furca, but the longest furca is found in Grasmere. The differences are, however, by no means sufficient to bridge the gap between *C. strenuus* and *C. abyssorum*.

It is rather remarkable that the colour of the Lakeland individuals is commonly a very pronounced yellow. The species has not, in fact, at all the general appearance of a limnetic form, but rather of an inhabitant of ponds and ditches.

#### *CYCLOPS VENUSTUS*, Norman & Scott.

Syn. *C. crinitus*, Graeter, 1908.

*Cyclops venustus* was described in 1906\* from specimens taken from marshy ground on Exmoor. It has since been found by Mr. D. J. Scourfield on Exmoor and Dartmoor, and by me in the Bog of Allen, near Newbridge in Ireland. It appears to be a species confined to lime-free waters, and may be included among what may be called the Sphagnophil Entomostraca, such as *Acantholeberis curcistrois*, *Chydorus piger*, *Moraria brevipes*, etc.

\* 'Crustacea of Devon and Cornwall,' p. 189 (London, 1906).

The description given by Norman and Scott is not altogether complete, inasmuch as no mention is made of the peculiar markings on the integument, which are quite distinctive, and the allusion to the swimming-feet as being similar to those of *C. vernalis* is misleading. It seems therefore advisable to supplement their description to some extent.

The most characteristic feature of the species is the very pronounced crenulation of the margins of the abdominal segments and (to a less extent) of the last thoracic segment. The surface of the integument of the thorax is marked by delicate striæ which give it the appearance of being minutely wrinkled, while the surface, both dorsal and ventral, of the abdominal segments is either striated or ornamented with lines of minute pits similar to those found in *C. diaphanus*. These pits seem to run, at least on the dorsal surface, on the crest of low ridges, which can be distinctly seen in side view. The furcal rami are provided, as in *C. viridis*, with cilia on their inner margins, but these cilia are in groups and do not form a continuous fringe. Usually the anal operculum is very prominent.

The swimming-legs differ markedly from those of *C. vernalis* not only in their more robust form, but also in the number of spines and setæ on the terminal joint of the outer ramus (see Table 9). But *C. vernalis* is subject to some variation in respect of the number of spines, and it is not unusual to find individuals with a spine-like formula of 3. 4. 4. 4. as in *C. venustus*; but in these cases the number of setæ is not increased. *C. vernalis* also resembles *C. venustus* in frequently having the cuticle of the abdominal segments pitted. The two species are, however, quite distinct, the form of the furca alone sufficing to distinguish them, apart from the differences in the form of the swimming-legs and the excessive pitting of the cuticle in *C. venustus*.

The resemblance to *C. capillatus*, Sars, is somewhat closer. The antennæ are 12-jointed in each species; the form of the receptaculum and the 5th leg is closely similar, and the spine- and seta-formula of the legs is identical. On the other hand, the legs of *C. capillatus* are distinctly more slender, and the furcal rami much more elongated and smooth on their inner edge. Further, though the abdominal segments show a slight toothling of the posterior margins, this is not pronounced, and I have not been able to detect any surface pitting in specimens from Norway which I collected many years ago in the Romsdal.

There remains for comparison the species described by Graeter in 1908 under the name of *C. crinitus*. M. Chappuis has been kind enough to send me a mounted specimen of this species, and an examination of this specimen and of the published descriptions of Graeter and Chappuis convinces me that the two species are identical. They agree in the following characters, wherein they differ from most other species:—

(1) Antennule of 12 joints.

(2) Furcal rami short, slightly divergent, with groups of cilia on their inner edge.

- (3) Median seta of the furcal rami of unusual length.
- (4) Outer seta of the furca of half (*crinitus*)\* or scarcely more than half (*venustus*) the length of the inner seta.
- (5) Swimming-legs with the same spine- and seta-formula † —a formula only found otherwise in *C. capillatus*, Sars.

Graeter states that the abdominal segments are jagged and that the surface of the cuticle is pitted over the whole body, but I have not been able to see this in the specimen, owing, no doubt, to its transparency.

Since Graeter's name is later than that of Norman and Scott, I have therefore regarded it as a synonym of *C. venustus*.

It is evident that this species and *C. viridis* are very closely related, as has already been pointed out both by Graeter and by Chappuis, but they are certainly distinct.

This species was found to be not uncommon in *Sphagnum* pools near Greendale Tarn and on Floutern Pass.

TABLE 9.—Showing spines and setæ on last joint of the exopodite in species of the *C. viridis*-group.

	Leg 1		2		3		4	
	Spines.	Setæ.	Spines.	Setæ.	Spines.	Setæ.	Spines.	Setæ.
<i>Cyclops venustus</i> , Norm. & Scott . . .	3	5	4	5	4	5	4	5
„ <i>crinitus</i> , Graeter . . . . .	..	..	4	..	4	..	4	5
„ <i>viridis</i> , Fischer . . . . .	2	4	3	4	3	4	3	4
„ <i>capillatus</i> , Sars . . . . .	3	5	4	5	4	5	4	5
„ <i>vernalis</i> , Fischer . . . . .	2	4	3	4	3	4	3	4
„ <i>vernalis</i> var. . . . .	3	4	4	4	4	4	4	4
„ <i>robustus</i> , Sars . . . . .	3	3	4	4	4	4	4	4

#### SIDA CRYSTALLINA, O. F. Muell.

*S. crystallina* is a littoral species not properly, or at least generally, belonging to the plankton, though frequently recorded as occurring in open water. In the Lake of Geneva, Lake Como, Lake Maggiore, and other

\* In the specimen which I have examined this seta is more than half the length of the inner seta, and so agrees completely with *C. venustus*.

† In the specimen at my disposal it is impossible to count the spines and setæ with certainty on all legs. I have given in the table only those which were beyond doubt.



large Swiss lakes, however, it appears to be a regular member of the plankton, and Burckhardt has described the form there found as a distinct species—*S. limnetica*, characterized chiefly by the absence of a nuchal organ.

In the Lake District it was found in small numbers in the majority of the collections from Derwentwater, so that it may probably be regarded as really limnetic there, whereas the few records of it from Bassenthwaite may be due simply to migration from the littoral region. The same is the case with Esthwaite and Grasmere. On the other hand, my experience of night collecting in Ennerdale seems to show that this species, though remaining in the littoral region during the day, may take to the open water at night. (See p. 422.)

All the specimens from the Lake District were of the typical form, with well-developed nuchal organ.

#### *HOLOPEDIUM GIBBERUM*, Zaddach.

The distribution of *Holopedium* in the Lake District is somewhat peculiar. It is recorded by Beck from Easedale Tarn (915 feet) and from Windermere, and it also occurs in Grasmere (P. A. Buxton, Sept. 1912) and Rydal Water (D. J. Scourfield). In Ullswater it was found in Sept. 1912 and on Aug. 20, 1920, but not in any other collection made by Dr. Pearsall. In Ennerdale it was present in very small numbers in three out of seven collections taken by him, but was abundant in my own collections in Sept. 1922. So far as is known at present it does not occur in any other lake in the district.

Easedale Tarn, Grasmere, Rydal, and Windermere form part of the same drainage system. The fact that it has so rarely been taken in Windermere may possibly be due to its being occasionally carried into the lake, but not becoming established there; but it is more probable that it is not uniformly distributed in the lake, and also that, being a deep-water form, it is not taken in surface plankton. In Ennerdale it is fairly evenly distributed in both shallow and deep parts, but it is rare on the surface during the day-time, preferring deep water. At night, however, it is abundant on the surface.

This preference for the deeper layers of water does not appear to be generally characteristic of the species, since Scheffelt (1908) states that it is found at the surface at all times; but he also found it to be unevenly distributed and to occur in swarms. Lilljeborg notes the same thing in Sweden.

It is generally regarded as a "Glacial relict," being confined to northern regions or to cold water.

#### *The genus DAPHNIA.*

The increase of knowledge of local and seasonal variation among the limnetic Daphnias has led to the general recognition that any division into well-defined species is impossible. All are therefore regarded as belonging to one species, *D. longispina*, within which an almost infinite number of

"subspecies," "varieties," and "forms" have been described. I do not propose to discuss the question of the systematic arrangement of these *Daphnias*, but it seems to me that the enlargement of the significance of the name *D. longispina* in this sense has serious disadvantages, and that the suggestion of Langhans that a new name, *D. variabilis*, should be introduced to include the whole series of these variable *Daphnias* might with advantage be adopted. The question can, however, hardly be regarded as finally settled, and, for the present, it is more satisfactory to accept Lilljeborg's *longispina*, *hyalina*, and *cucullata*, whilst fully recognising that the three are united by transitional forms.

All the limnetic *Daphnias* of the lakes belong to the "species" *hyalina* with its "subspecies" *galeata* and *lacustris*. Beck has recorded the occurrence of *D. cucullata* (under the name *Hyalodaphnia berolinensis*), but this species has been seen in the district by no one else, and it is probable that he was mistaken. *Daphnia* is absent altogether from Wastwater and Ennerdale Water, and apparently also normally from Bassenthwaite. There are none from the latter lake either in Dr. Pearsall's collections or my own, and Mr. Scourfield informs me that he also failed to find it there. On the other hand, Miss Pratt records both *D. pulex* and *D. longispina* as occurring in April 1898, so that apparently some species occurs there at times. As Bassenthwaite receives the overflow from Derwentwater which contains an abundance of *Daphnia*, it is very remarkable that the same form should not establish itself in Bassenthwaite.

The distribution of the different forms of *Daphnia* in the district seems to bear little or no relation to the drainage system. While Buttermere and Crummock, which were originally united into one lake, both contain the typical *D. hyalina*, which occurs in these lakes only, the *Daphnia* of Esthwaite is quite different from that of Windermere, into which Esthwaite drains, and the same form, *D. galeata*, inhabits Windermere and Coniston, which are not connected in any way.

#### DAPHNIA HYALINA s. str., in Buttermere and Crummock.

In the form from these two lakes the front of the head is usually very nearly straight or slightly concave (text-fig. 3, A); but it is very variable, and may occasionally be distinctly convex as in *D. pellucida*. In a collection made on Aug. 27, 1920, several specimens were seen with the front of the form shown in text-fig. 3, B. An exactly similar variety is illustrated by Lilljeborg (1900, pl. xv. fig. 4) as "*formaestivalis monstrosa*." It is characteristic of the Crummock *Daphnias* that the shell-spine forms a considerable angle with the body axis—from 20°–40°. Although I regard this form of *Daphnia* as properly referable to *D. hyalina* s. str., Lilljeborg, in some respects the population is transitional on the one hand to *D. lacustris* and on the other to *D. pellucida*.

In a plankton sample of Sept. 1912 a single specimen was met with which obviously belongs to *D. galeata* (text-fig. 3, C). I do not think that this specimen can be regarded as a sport or mutation from *D. hyalina*, but rather as an instance of the transport of an ephippium from Coniston or Windermere. If this be so it goes to show that these lakes are not so isolated as would appear, and that interchange of species is not infrequent. If, in spite of such interchange, the *Daphnias* inhabiting the different lakes remain distinct, it is evident that the local races are established by right of survival, and it leads one to suppose that, difficult as they may be to separate, yet they may represent fixed species. Our conception of species is determined mainly by our ability to discriminate individuals by fixed and measurable standards; but not only are physiological differences largely ignored or are unmeasurable, but two races separated only by minimal mean differences may be just as real specific units as those distinguished by obvious characters in all individuals. The evidence goes to show that a single lake as a rule is inhabited by one race of limnetic *Daphnia* only, and, although within such a race extreme forms are commonly found, it is obviously of no use to give these variants names, as has frequently been done in the past. But, with that exception, it seems advisable in the present state of knowledge to recognize all well-marked races as distinct rather than to treat all as variants of one collective species. The question of real specific distinction cannot, I think, be determined by laboratory experiment, neither is the fact that the winter forms of a number of *Daphnias* can be shown to be morphologically identical prove anything more than close relationship. If the many forms of *Daphnia* are to be regarded as variants of one species originating under the influence of external conditions, the reappearance in widely-separated areas and under conditions which can hardly be imagined to be identical of precisely the same form—e. g. *D. galeata* in Windermere and in Central Asia—is difficult or impossible to understand. It must be admitted that the whole problem of specific validity is raised by the genus *Daphnia* in its acutest form, and is far from being solved.

#### DAPHNIA LACUSTRIS, *Sars*.

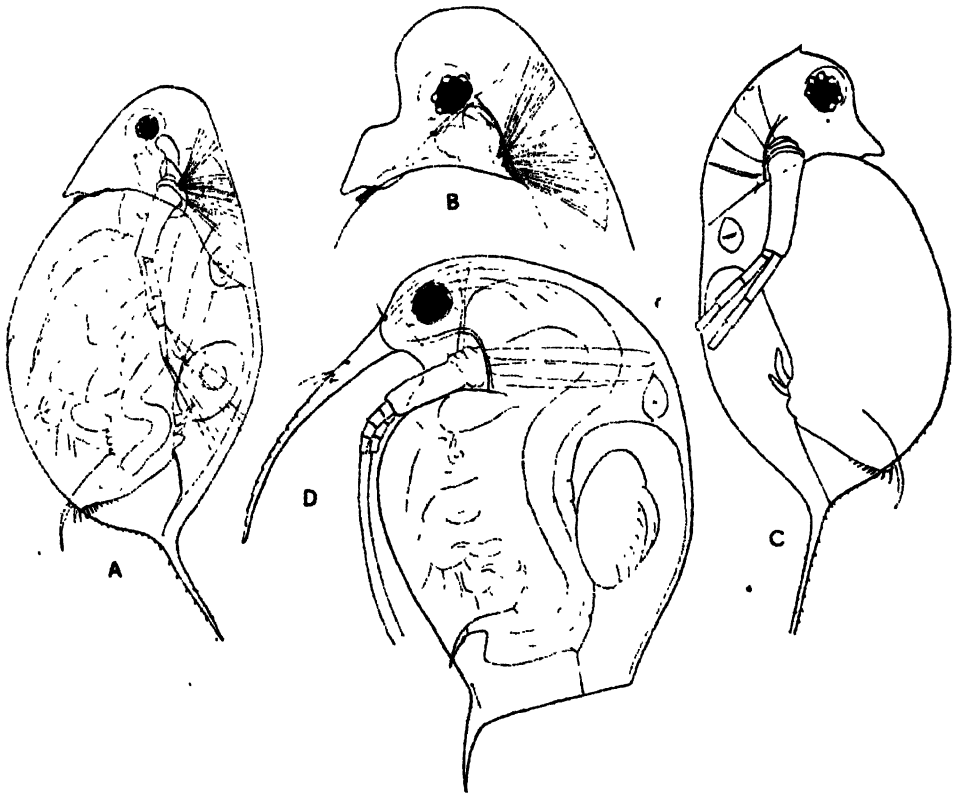
##### 1. Esthwaite and Hawes Water.

The *Daphnias* of Esthwaite illustrate remarkably well the impossibility of drawing any definite distinction between the various forms now grouped within the species *D. longispina*. While some individuals taken in Esthwaite in July 1921 were indistinguishable from *D. longispina* forma *rosea*, having the crest interrupted over the eye and the general form of that species, the usual type of *Daphnia* present in that and in other collections belongs to *D. hyalina* var. *lacustris*. I was at first inclined to suppose that two distinct races were present, but the two forms grade so completely one into the other that they must be regarded as one. The outline of the head may be completely rounded, or may show a scarcely noticeable dorsal angle, while in

others, and especially in young specimens, this angle is produced into a small papilliform projection. The crest is generally continuous over the eye, but is often so inconspicuous as to be seen with difficulty, while sometimes it is interrupted as in *D. longispina*.

An exactly similar *Daphnia* occurs in Hawes Water, but in such small numbers that I have not had much material for examination. Nearly all the

FIG. 3.



- A. *Daphnia hyalina* from Crummock, 29.9.22. Typical form for the lake.  
 B. *Daphnia hyalina* from Crummock, 27.8.20. Head of female of Lilljeborg's  
*forma aestivalis monstrosa*.  
 C. *Daphnia galeata* from Crummock, Sept. 1912.  
 D. *Bosmina obtusirostris* from Wastwater, 30.9.22.

specimens seen have the head quite rounded, but occasionally there is a slight trace of the dorsal angle so often seen in Esthwaite specimens.

This form seems to be the same as that which is found in Loch Leven and Loch Lomond in Scotland, and was described by Richard (1896, p. 307) as *D. lacustris* var. *vicina*, with the exception that the posterior spine in the Lake District form is usually directed more or less dorsally.

Burckhardt's *D. hyalina* forma *lucernensis* from the Lake of Lucerne is evidently the same variety. In one individual from Esthwaite the dorsal projection of the head is denticulate as figured by Burckhardt for his forma *jurassica*.

#### Derwentwater.

The Daphnias from Derwentwater rather closely resemble *D. hyalina* s. str., but should, I think, rather be included in *D. lacustris* by reason of the concave front and rather higher head. The dorsal angle characteristic of the form from Esthwaite and Hawes Water is occasionally, but very rarely, seen in Derwentwater.

#### DAPHNIA GALEATA, Sars.

The typical form of *D. galeata* occurs throughout the year in Coniston, Windermere, and Ullswater, being most abundant in the former. Although Dr. Pearsall's samples cover every season in the year, I have not found ephippial females in any of them, so that the species appears to be acyclic. The same appears to be the case with the *D. lacustris* of Esthwaite, Hawes Water, and Derwentwater, but in Crummock and Buttermere there is a distinct sexual phase in *D. hyalina* in October, though, even here, the species persists through the winter.

#### *Daphnia*—Seasonal Variation.

The material at my disposal does not admit of any positive statement with regard to seasonal variation of form, but such variation is very slight if it occurs at all. With regard to *D. galeata*, in which it could most easily be detected, I have found on the one hand crests equally as high in winter as in summer, and individuals with a quite round head in July and August. I have no doubt that a small variation of head-form, and of size of body, could be shown statistically with sufficient material, but the variation is certainly not so pronounced as to be appreciable to the eye.

In this respect also the plankton of these lakes differs markedly from the Danish and Central European lakes, and approaches the northern type.

#### BOSMINA OBTUSIROSTRIS, Sars.

The identity of the northern races of *B. coregoni* with those occurring in the alpine lakes is now established, and, according to Rühe, the united species should be known under the name of *B. coregoni-longispina*. As, however, the name *B. longispina* has generally been used in a more restricted sense, and is so used by Lilljeborg, and as the name *B. obtusirostris* has been universally used for the northern forms with short mucro, I prefer to retain it in Lilljeborg's sense.

In the Lake District this species occurs, often in great abundance, in nearly all the lakes. Its apparent absence from Buttermere may be due to the fact that the collections were made from the shore only; but, although a single

specimen was found in Bassenthwaite in October 1921, it is certainly not established there.

It would be of interest to ascertain if there are any constant differences between the *Bosminas* of the different lakes, but this can only be done satisfactorily by measurements of large numbers of specimens carried out on the system laid down by Burckhardt, and my material does not admit of such treatment, since the necessary number of well-preserved specimens is not available from all the lakes at the same seasons. Since there is very great variability within the population of a lake with regard to length of antenna and of mucro, the selection of single individuals for measurement or illustration is likely to be misleading, but it is not entirely without value,

TABLE 10.—Measurements of single individuals of  
*Bosmina obtusirostris*.

	Date.	Length.	Shell.		Length of antenna.	Length of mucro.
			Length.	Width.		
Windermere . . . . .	21. vii.	·63	743	784	310	81
Esthwaite . . . . .	3. ix.	·6	726	712	328	96
Derwentwater . . .	17. v.	·64	703	750	390	98
Ullswater . . . . .	1. vii.	·65	753	753	430	92
Hawes Water . . .	11. vii.	·6	716	783	333	66
Coniston . . . . .	5. vii.	·68	706	647	404	110
Ennerdale . . . . .	28. ix.	·66	712	788	393	45
Wastwater . . . . .	30. ix.	·92	717	706	543	152
Crummock . . . . .	12. vii.	·89	707	752	505	123
Flouthern Tarn . . .	27. ix.	·52	711	711	327	38
Goats Water . . . .	3. x.	·53	754	717	490	19

and a table of measurements of individuals chosen as being so far as could be judged typical of the population is here given. The example given from Esthwaite is above and that from Ennerdale below the average size, but typical of form. This table shows that the *Bosminas* of the two primitive lakes Crummock and Wastwater are not only very much larger than all others, but have longer mucro and antenna (text-fig. 3, D). On the other hand, those from Ennerdale, which might be expected to be similar to those from Wastwater, are, in fact, conspicuous for their very short antenna and mucro and are not particularly large. Herein is another strong point of difference between these two apparently similar lakes. In the remainder of the lakes the differences shown between the *Bosminas* are not, I think, outside the limits of their ordinary variation within a single population. The specimens from Flouthern Tarn and Goats Water are not only the smallest, but have the shortest mucro.

For the reasons given above I have also been unable to study the seasonal variation. I have, it is true, made an attempt to do so with material from Coniston, but the numbers available and sufficiently well preserved are not enough to give a satisfactory result. They tend to show that there is a variation, but that it is very small.

The species is found at all times of the year, and, except in Wastwater and the tarns, there seem to be no pronounced sexual periods. Ephippial females have been seen in collections from Windermere (Sept. and Oct. 1921), Crummock (Oct. 1921), Derwentwater (Nov. 1921), and Wastwater (Sept. and Oct. 1921 and 1922). In Wastwater alone do ephippial females form any considerable proportion of the population. On Sept. 30, 1922, 31 per cent. of females were ephippial, but not a single male was seen. In Coniston and Ullswater there seems to be no sexual phase.

*BOSMINA LONGIROSTRIS*, (L. F. Muell.

This species only occurs in Esthwaite and Grasmere, both being lakes of the "evolved" type; but, whereas it appears to be the only species of *Bosmina* in Grasmere, in Esthwaite it is found in company with *B. obtusirostris*, an unusual association which is also found in Lough Neagh and has been commented on by Dakin and Lataurche.

Miss Pratt states that it was common in Bassenthwaite in 1898, but it was not found in any of Dr. Pearsall's collections from that lake. Miss Pratt's list of Crustacea from Bassenthwaite differs in so many respects from my own that one can only conclude that conditions must have changed very greatly since 1898.

The Esthwaite form is quite typical, but in Sept. 1921 the antennæ of the adults were found to be unusually short, and many were even of the form described by Lilljeborg under the name of *B. brevicornis* Hellich. It appeared in the collections first in April and increased in numbers till June. In July numbers decreased, and in August it was very rare. In September it was again present in abundance, and large numbers of females bore ephippia. It was not found in collections made in October and November.

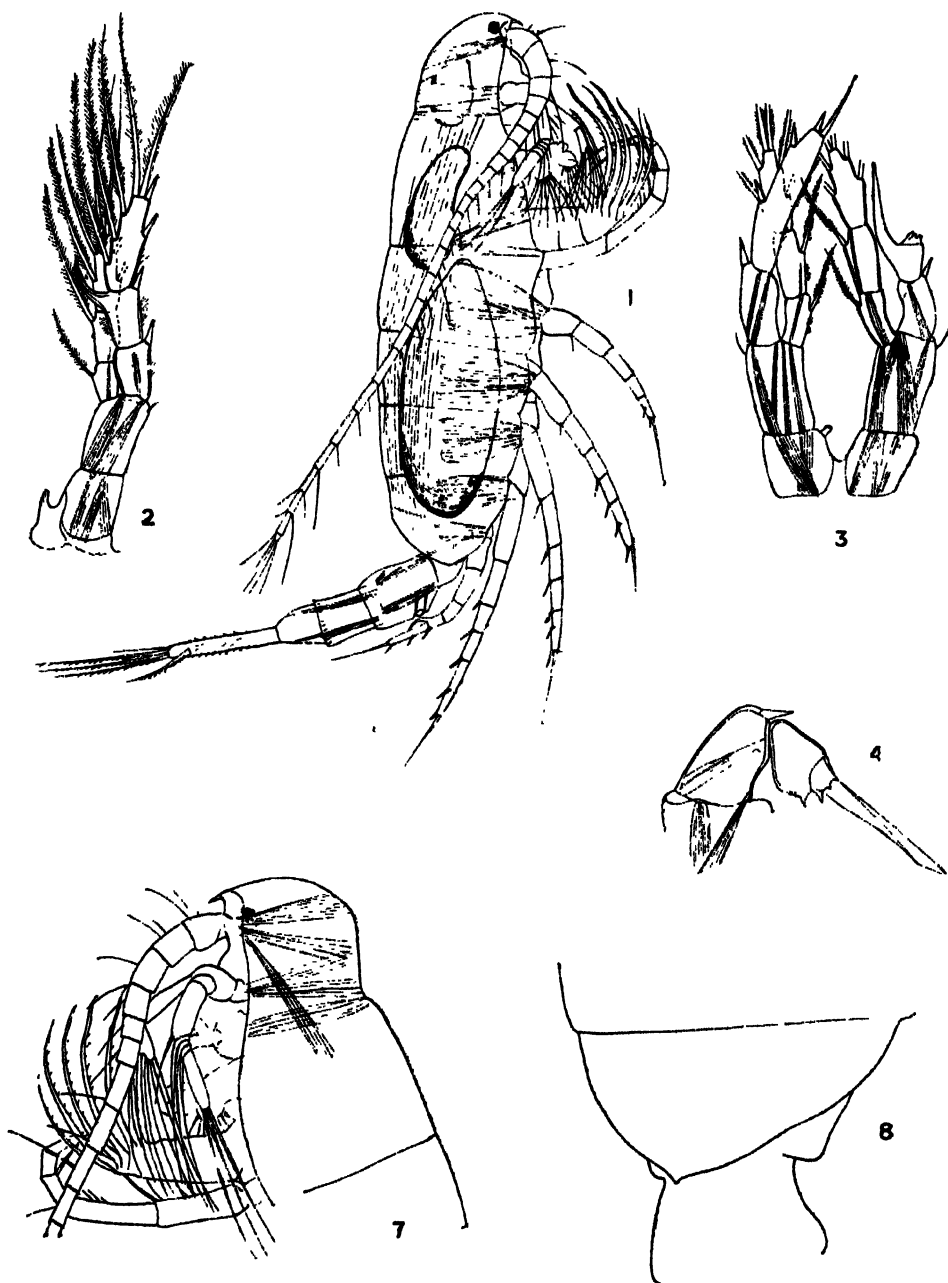
LITERATURE REFERRED TO.

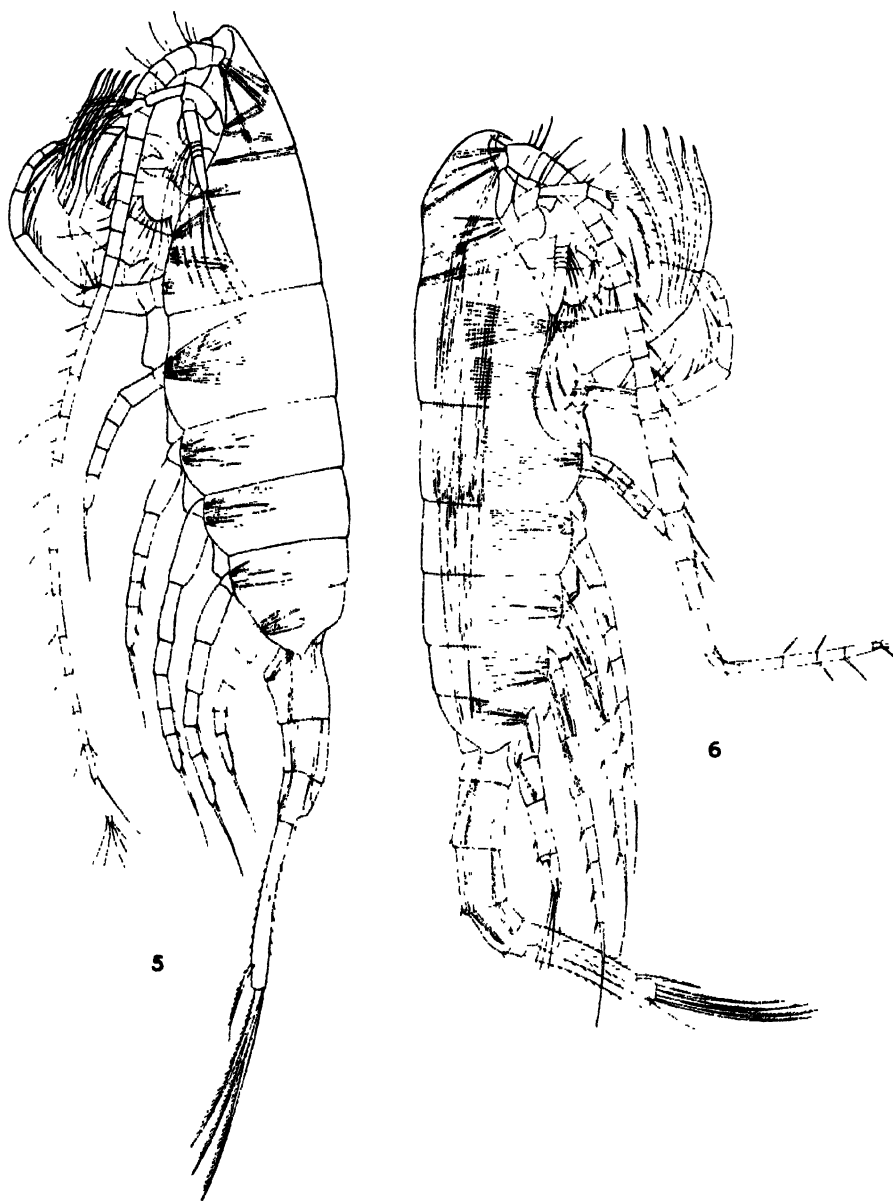
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## EXPLANATION OF PLATE 23

*Limnocalanus macrurus*, Sars

- Fig. 1 Side view of female from Luncerdale Water  
 2 Fifth leg of female  
 3 Fifth leg of male  
 4 Outer branch of right fifth leg of male  
 5 Side view of female from the Caspian Sea (*L. grimaldus*)  
 6 Side view of male from Lake Erie  
 7 Head of female from Inarjon, Sweden  
 8 Side view of last thoracic segment of male from Lake Malaren, Sweden



Some Protozoa from the Soils and Mosses of Spitsbergen. Results of the Oxford University Expedition to Spitsbergen, No. 27.  
By H. SANDON. (Communicated by D. WARD CUTLER, F.L.S.)

[From the Protozoology Department, Rothamsted.]

(PLATE 24 and 6 Text-figures.)

[Read 7th June, 1923.]

THE protozoal fauna of Spitsbergen and of the neighbouring lands is in some respects already fairly well known. As far back as 1869, Ehrenberg (14) identified four species in material brought back from there, and more recently Scourfield (29) and Penard (23) have published extensive lists of collections from Advent Bay, Green Harbour, and Amsterdam Is. The establishment of a biological station on the Murmansk coast enabled Awerinzew (24) to carry out investigations of the protozoa of that region, and his collections extended as far as Bear Island, the southernmost island of the Spitsbergen Archipelago; while Mereschkowski (19) and Levander (18) have also identified numerous species from the northern parts of Finland, Russia, and Siberia. Scourfield, Penard, and Awerinzew, however, confined their attention entirely to the inhabitants of mosses, and in particular to the testaceous rhizopods, and none of the authors since Ehrenberg have investigated the soil-dwelling forms. It has recently been shown that in temperate lands protozoa inhabit the soil in such large numbers that they must play an important part in the activities of the soil (see especially 12); and a knowledge of the soil protozoa from localities subject to extreme climatic conditions therefore assumes considerable interest, not only in relation to the general ecological problems of those regions, but also because of the light it may be expected to throw on the influence of climatic conditions on the soil organisms.

The material kindly placed at my disposal by the members of the Oxford University Expedition consisted of three samples of mud from the brackish pools near Bruce City described by Walton (33), five samples of soils from various localities, and fifteen samples of mosses; and the supplementary expedition of 1922 also brought back three samples of soil. The soil samples were all packed in tightly-fitting tins which had previously been sterilised by heat, and the mosses had been dried and sealed up in envelopes.

## METHODS.

Cultures were made from all the samples on plates of nutrient agar, in sterile tap-water, and dilute hay infusion, and were examined at intervals for three or four weeks. For detecting rhizopod tests, soil or moss was taken from the tap-water cultures after a few days, spread out on a glass slide and examined with a low power, the mosses being first teased apart with a needle.

## RESULTS.

## 1. MUD.

These samples gave very disappointing results, possibly owing to excessive heat having been employed during drying. *Heteromita globosa* was found in all of them, and *Sainouron mikroteron* (n. g., n. sp.) (see Appendix) in the mud from pond 5, the least saline of the three. Since the members of the expedition recorded the presence of peridinians in some of these ponds, cultures in Miquel's solution (1) were made at the kind suggestion of Dr. E. J. Allen in the hopes of obtaining growths of these organisms, but, again, only the ubiquitous *Heteromita globosa* and some diatoms were found.

In his notes made on the spot Mr. Elton records that *Uroglena volvox* was very abundant in all the ponds in this district, and that there were also found flagellates belonging to the genera *Euglena* and *Glenodinium*, and ciliates probably belonging to the genera *Vorticella*, *Carchesium*, *Dileptus*, *Prorodon*, and *Colpoda*. He makes the further interesting observation that whereas in the Bruce City ponds, which were fed with drainage water from limestone hills, *Uroglena* was very abundant, at Cape Bohemian, where the pools were in sandstone, this species was absent, and its place was taken by large numbers of *Synura uvella* and of peridinians. From the latter region his records also include *Glenodinium* sp., *Euglena* sp., and three ciliates, probably *Spathidium*, *Nassula*, and *Ophrydium*.

## 2. SOILS.

As will be seen from the accompanying table (pp. 456-457), the 1921 soil samples form an interesting series. Apart from rhizopod shells, soil I yielded only two species, and in fact three out of the six cultures made from this sample were completely sterile. The number of species recorded from sample 5, on the other hand, is quite comparable to that which would be found in any British farm or garden soil, while the other samples fall between these two extremes. Soil 1, however, contained great numbers of empty rhizopod tests belonging to six different species, whereas in the other samples these organisms were much less abundant.

An attempt was made to connect these striking differences with other characteristics of the soils. The bacterial numbers, counted as they were

after the soil had been sealed in tins for some months, are of course no indication of the actual number of bacteria in the soils at the time when the samples were taken, but for purely comparative purposes they no doubt correspond to real differences in the bacterial population of the soils. The chemical and physical properties of the soils, however, throw no light on these differences. The high numbers of organisms found in soil 5 may be attributed to the sea-birds' droppings with which it was manured; but, on the other hand, soil 4 was similarly manured, and yet yielded fewer organisms than soil 3, which was practically free from humus. The abundance of rhizopod tests in soil 1 corresponds closely with what is found in peaty soils elsewhere (20). It is possible that this does not really indicate a larger active population of these organisms than in other soils, but is due simply to the fact that in a soil, where microbial activity is small, such tests, coming either from animals living in the soil, or being brought down from the mosses etc. growing in it, disintegrate more slowly than in other soils, and so accumulate in considerable numbers.

The 1922 samples were examined in a fresher condition than those of the previous year, and on the whole yielded a considerably larger number of living species. The good results obtained from sample 5 (1921), however, seem to indicate that these earlier samples had not suffered appreciably as a result of storage, and the difference in the results obtained from the two sets of samples probably therefore corresponds with an actual difference in the population of the soils *in situ*. Sample 3 (1922) was taken with a view to confirming the results obtained from sample 1 (1921), in which both bacteria and protozoa were so exceptionally few. Unfortunately it was not possible to bring soil from the identical spot, and although the localities from which the two samples were obtained appeared very similar and supported a similar type of vegetation, the analysis given in the table (p. 456) shows that the two soils are not really comparable.

The abundance of protozoa in samples 1 and 3 (1922) is of particular interest, in view of the high acidity of these soils. Such results, however, are not unique, for an active protozoal population has been found by Mlle. Perey in the soil of one of the Rothamsted experimental plots for which the pH is 3.65; and S. M. Nasir (in some unpublished work also done in this laboratory) has found that in artificial cultures active flagellates can tolerate a pH of 4.5, active amœbæ a pH of 3.9, while ciliates can grow even when the acidity is as high as that represented by a pH value of 3.5.

### 3. MOSSES.

Twelve of the samples came from Klaas Billen Bay, and were composed of the following mosses:—*Hypnum* (5 spp.), *Cinclidium stygium*, *Orthothecium chryseum*, *Swartzia montana*, *Bryum* spp., *Camptothecium nitens*, *Grimmia*



*commutata*, and *Brachytherium salebrosum*. Most of the samples were composed of a mixture of two or three of these mosses. The remaining three samples came from Prince Charles Foreland, and were composed of *Rhacomitrium lanuginosum*, *R. canescens* var. *ericoides*, and *Dicranum groenlandicum*.

### Flagellata.

<i>Cercomonas crassicauda</i> Alexeieff.	In	3 samples from Klaas Billen Bay,	and in	0 samples from Prince Charles Foreland.
<i>Oocomonas termo</i> Kent.	2	" " "	"	1 " " "
<i>Heteromita globosa</i> Stein	11	" " "	"	2 " " "
" <i>lens</i> Müller	1	" " "	"	0 " " "
<i>Spiromonas angusta</i> (Duj.) Kent.	1	" " "	"	0 " " "
<i>Helkesimastix fecicola</i> Woodcock & Lapage	1	" " "	"	0 " " "
<i>Phyllomitus</i> sp.	1	" " "	"	0 " " "
<i>Anisonema minus</i> (n. sp.)	1	" " "	"	0 " " "
<i>Entosiphon sulcatum</i> (Duj.) Stein	1	" " "	"	0 " " "
<i>Saia uron orn</i> (n. g., n. sp.)	2	" " "	"	1(?) " " "
<i>Allantion tachyploon</i> (n. g., n. sp.)	2	" " "	"	0 " " "

Most of these species are identical with those found in the soil samples. This is perhaps not surprising, as most of the mosses had a certain amount of soil clinging to them, and no attempt was made to remove this before making the cultures. Hence it is impossible to say whether the organisms found naturally inhabited the surface of the moss plants or the soil in which the latter were growing.

### Rhizopoda.

<i>Hartmanella hyalina</i> Alexeieff	In	3 samples from Klaas Billen Bay,	and in	0 samples from Prince Charles Foreland.
<i>Ameba limicola</i> Rhumbler	1	" " "	"	0 " " "
Sp. a (Cutler, Cramp, & Sandon)	1	" " "	"	0 " " "
<i>Amoeba vesperilio</i> Penard	1	" " "	"	1(?) " " "
" <i>terricola</i> Greef	1	" " "	"	0 " " "
" <i>striata</i> Penard	1(?)	" " "	"	0 " " "
" <i>actinophora</i> Auerb.	1	" " "	"	0 " " "
<i>Orycia flava</i> Greef	1	" " "	"	1 " " "
" <i>coronatu</i> var. <i>simplex</i> [Penard]	1	" " "	"	0 " " "
<i>Diffugia pyriformis</i> Perty	8	" " "	"	0 " " "
" <i>fallax</i> Penard	7	" " "	"	1 " " "
" <i>globulus</i> Duj.	6	" " "	"	3 " " "
" <i>lucida</i> Penard	1	" " "	"	0 " " "
" <i>constricta</i> Ehrenb.	11	" " "	"	3 " " "
<i>Centropyxis aculeata</i> Stein	5	" " "	"	0 " " "
" <i>laevigata</i> Penard	5	" " "	"	0 " " "
<i>Arcella vulgaris</i> Ehrenb.	3	" " "	"	0 " " "
" <i>arenaria</i> Greef	1	" " "	"	1 " " "

<i>Nebela collaris</i> Leidy . . . . .		In 6 samples from Klaas Billen Bay, {		and in 0 samples from Prince Charles Foreland.	
<i>Quadrula irregularis</i> Archer . . . . .	8	"	"	0	"
<i>Euglypha ciliata</i> Ehrenb. . . . .	4	"	"	0	"
" <i>strigosa</i> Leidy . . . . .	1	"	"	0	"
" " var. <i>glabra</i> [Wailes . . . . .	1	"	"	2	"
" <i>levis</i> Party . . . . .	1(±3)	"	"	1	"
" <i>tuberculata</i> Duj. . . . .	0	"	"	1	"
<i>Assulina muscorum</i> (Tereb.) . . . . .	0	"	"	2	"
<i>Cyphoderia</i> sp., Schlumb. . . . .	3	"	"	0	"
<i>Campanus triqueter</i> Penard . . . . .	3	"	"	0	"
<i>Trinema enchelys</i> Ehrenb. . . . .	3	"	"	0	"
" " var. <i>galeata</i> [Penard . . . . .	1	"	"	0	"
" <i>complanatum</i> Penard . . . . .	1	"	"	2	"
" <i>lineare</i> Penard . . . . .	6	"	"	1	"
<i>Corythion dubium</i> Taranek . . . . .	0	"	"	2	"
<i>Chlamydothryx stercorea</i> Cienk. . . . .	1	"	"	1	"

### Ciliata.

Of the samples from Klaas Billen Bay, six contained *Colpoda cucullus* O. F. Muell., two contained *Balantiophorus minutus* Schew., and the following forms occurred in one sample each:—*Balantiophorus elongatus* Schew., *Blepharisma laterita* Ehrenb., *Cyclidium glaucoma* Ehrenb., *Enchelys* sp., *Oxytricha* sp., *Stylonychia* sp. In the soils from Prince Charles Foreland only *Colpoda cucullus* O. F. Muell. was found.

### DISCUSSION.

#### (1) *The Influence of Arctic Conditions on Protozoa.*

Previous investigators have differed considerably as to the influence of arctic conditions on protozoa. Although the ubiquity of most of the commoner fresh-water and moss-dwelling species is well known, it is rather difficult to believe that the same species can live in arctic as in temperate and even tropical lands without showing some local peculiarities. It was perhaps this consideration which led Ehrenberg (15) to create new specific names for the rhizopod shells obtained from Greenland, which names have since apparently all been discarded. Scourfield (29) remarks on the numbers of abnormal tests (especially in the species *Euglypha ciliata* and *Nebela collaris*) found in his Spitsbergen material, and Penard (26) similarly comments on the tendency to produce deviations from the type in the rhizopods from the still more extreme regions of the antarctic. On the other hand, whereas Penard's antarctic specimens were mostly smaller than the average (especially in the genera *Assulina*, *Corycia*, *Corythion*, and *Euglypha*), Awerinzew (2)

found that tests from north polar regions were on the whole larger than the average.

The present investigation throws little light on this question. Several species (e.g. *Arcella arenaria*, *Trinema complanatum*) included some exceptionally big specimens, but others were on the average rather below the normal size (*Centropyxis aculeata*, *C. lavigata*, *Nebela collaris*). Observations of this kind are, however, very inconclusive unless based on statistical data; and as no such data from temperate regions are available for comparison, there was no point in devoting time to obtaining them from the present material. It seems, however, fairly certain that there is no general tendency to either a larger or a smaller size in the Spitsbergen rhizopods, and that none of the species found formed any distinctive local varieties.

## (2) *Species recorded.*

The rhizopods commonly found living on mosses have been divided by Penard (24) into two groups which he calls respectively "formes banales" (*i.e.* forms commonly found in mosses but not especially adapted to such a life) and "formes caractéristiques" (*i.e.* forms specially adapted to living among mosses and rarely found elsewhere). The former group contains 26 species, of which 21 have now been recorded from Spitsbergen; but of the second group, only 2 out of 17 have so far been found there, and one of these is *Amoeba terricola*, which seems out of place in this classification, since, so far from being specially adapted to living among mosses, it occurs frequently, as its name implies, in soil. The absence of the "formes caractéristiques" is probably due in part to the fact that they include a number of naked amœbæ which do not normally form cysts, and which therefore may have been present in the moss when it was collected, but died before the samples were examined.

Løvander (18) and Heinis (16) have already drawn attention to the close similarity existing between the rhizopod fauna of the high latitudes and that of the high altitudes of the European Alps, as recorded by Zschokke (37), Daday (13), and Heinis (16). The present investigation completely confirms this analogy, but unfortunately the data available do not appear to be sufficiently complete to extend it to other groups of protozoa. The generalisation that Heinis makes with respect to the high Alpine protozoa, however, seems to apply equally to the Spitsbergen records: namely, that the severity of the climate does not result in the occurrence of local species, but simply eliminates the less adaptable forms, with the result that the population is composed of the most cosmopolitan forms. The possibility of the existence of true arctic species is, however, not entirely ruled out by these considerations (except in the testaceous forms), since such species, if they exist, may have died out completely before the material could be examined.

One new flagellate is described which does not seem to have been recorded elsewhere, and it is possible that some of the organisms which occurred in the cultures in too small numbers to be identifiable may have represented other new species.

The ubiquity of these moss- and soil-dwelling protozoa has an additional significance, since they have no means of avoiding the extremes of temperature or of moisture to which they are exposed. Planktonic organisms can avoid extreme heat or cold by sinking to greater depths, and worms, many insects, etc., can similarly burrow to more equable layers if the surface of the soil becomes too hot or too cold except, of course, in regions where the sub-soil is frozen. But such vertical migrations of the land-living protozoa, if they take place at all, must be very much more restricted, and the wide distribution of these organisms must therefore indicate a wide range of tolerance of external conditions on the part of the organisms themselves or of their cysts (though resistant cysts are not at present known for all the creatures in question). There remains the possibility of the existence of physiological strains differing solely in their powers of resisting extreme conditions. This is, in fact, very probable, since many unpublished observations made in this laboratory have demonstrated the presence in tropical soils (Egypt, East Africa, West Indies, etc.) of species identical with some occurring in Spitsbergen, which therefore in natural conditions tolerate a wider range of temperatures than is possible in laboratory cultures.

The identity of the protozoal fauna of Spitsbergen with that of temperate lands is strikingly paralleled by the observations made by Barthel (5) on the soil bacteria of Greenland. An examination of soils collected by the Rasmussen Expedition from Disko Is. (Lat.  $70^{\circ}$  N.), from Cape York (Lat.  $76^{\circ}$  N.), and from the extreme northern coast showed that these soils, just like ordinary European soils, are capable of initiating the processes of nitrification, denitrification, ammonification, and fermentation of urea; and though nitrogen fixation was not definitely proved, there was some evidence of its occurrence. These results would no doubt apply equally in the somewhat milder climate of Spitsbergen. Thus all the evidence at present available points to the qualitative identity of the microbiological activity of soils from Spitsbergen and from temperate lands. As to the quantitative aspects of the question, observations made on the spot would be essential.

Sample.	Locality.	Description.	% dry matter.	% N in dry matter.	% loss on ignition.
1921. 1.	Low hill near coast, Prince Charles Foreland.	Black peat containing roots, etc. Dry tundra vegetation ( <i>Silene</i> , <i>Salix</i> , mosses, etc.).	90.1	1.53	51.9
2.	Klaas Billen Bay.	Fine black loam from roots of <i>Andromeda</i> .	94.9	0.75	27.9
3.	Klaas Billen Bay.	Stony calcareous soil from roots of <i>Dryas</i> ; practically no humus but much dry plant-remains.	98.9	0.152	32.8
4.	Moss plain below Vogel Hook (Pr. Charles Foreland).	Damp mossy peat, much manured by sea-birds' droppings.	88.4	2.85	69.5
5.	Vogel Hook.	Fine brown peat, much manured by sea-birds' droppings.	91.2	2.47	47.3
1922. 1.	Grassy slopes on bird cliffs, Green Mt., Ice Fiord.	The grass here is more luxuriant than anywhere else on the island.	48.6	1.485	38.94
2.	Boggy patch on hillside at Advent Valley, Ice Fiord.	Vegetation <i>Sphagnum</i> etc.	44.1	0.440	22.42
3.	Dry tundra at foot of hills, Advent Valley.	Vegetation <i>Dryas</i> , <i>Salix polaris</i> , <i>Silene</i> , etc. Well-rotted mould.	79.71	0.378	13.82

pH.	No. of bacteria per gramme (millions).	FLAGELLATA.	CILIATA.	RHIZOPODA.
6.3	1.3	<i>Heteromita lens</i> .	<i>Colpoda cucullus</i> .	<i>Diffugia globulus</i> , <i>D. constricta</i> , <i>Euglypha laevis</i> , <i>Assulina muscorum</i> , <i>Hyalosphenia minuta</i> .
7.2	4.87	<i>Oicomonas termo</i> , <i>Heteromita globosa</i> , <i>Cercomonas</i> sp.	<i>Balantiophorus minutus</i> , <i>Uroleptus mobilis</i> , and an unidentified species.	<i>Amoeba radiosa</i> , <i>Diffugia constricta</i> , <i>Centropygeis larigata</i> , <i>Quadrula irregularis</i> .
8.0	12.65	<i>Heteromita globosa</i> , <i>Cryptomonas obovoides</i> .	<i>Colpoda cucullus</i> , <i>Cyclidium glaucoma</i> , <i>Pleurotricha</i> sp., <i>Vorticella microstoma</i> .	<i>Diffugia constricta</i> , <i>Diffugia</i> sp.
6.6	6.25	<i>Heteromita globosa</i> , <i>H. lens</i> .	<i>Colpoda cucullus</i> , <i>Gonostomum affine</i> .	<i>Amoeba limax</i> , <i>A. radiosa</i> , <i>A. terricola</i> , <i>Diffugia globulus</i> , <i>D. constricta</i> .
6.0	5.45	<i>Oicomonas termo</i> , <i>Heteromita globosa</i> , <i>H. lens</i> , <i>Cercomonas crassicauda</i> , <i>Helkesimastix faecicola</i> , <i>Copromonas</i> sp., <i>Cladomonas fruticosa</i> .	<i>Colpoda cucullus</i> , <i>Uronema</i> sp., <i>Oxytricha pellionella</i> , <i>Blepharisma lateralis</i> , and one unidentified species.	<i>Dimastigamoeba gruberi</i> , <i>Hartmannella hyalina</i> , <i>A. diploidea</i> , <i>A. terricola</i> , <i>A. sp.</i> , <i>Nuclearia simplex</i> , <i>Chlamydothrys stercorea</i> , <i>Diffugia globulus</i> , <i>D. constricta</i> , <i>Centropygeis larigata</i> , <i>Euglypha strigosa</i> .
3.9		<i>Oicomonas termo</i> , <i>Heteromita globosa</i> , „ <i>lens</i> , <i>Cercomonas</i> sp.	<i>Chilodon cucullulus</i> , <i>Enchelys</i> (probably <i>E. farcimen</i> ), <i>Vorticella microstoma</i> , <i>Oxytricha pellionella</i> , and 3 unidentified species.	<i>Amoeba limax</i> , <i>A. radiosa</i> , <i>A. diploidea</i> , <i>A. terricola</i> , <i>A. actinophora</i> , <i>Nuclearia simplex</i> , <i>Chlamydothrys stercorea</i> , <i>Trinema lineare</i> , <i>Diffugia constricta</i> , <i>D. globulus</i> , <i>D. fallax</i> , <i>Nebela lageniformis</i> , <i>Euglypha</i> sp., <i>Assulina muscorum</i> .
6.0		<i>Oicomonas termo</i> , <i>Heteromita lens</i> , <i>Cercomonas</i> sp., <i>Sp. ?</i> .	<i>Enchelys</i> (probably <i>E. farcimen</i> ).	<i>Amoeba limax</i> , <i>Trinema lineare</i> , <i>T. enchelys</i> , <i>Diffugia constricta</i> , <i>D. globulus</i> , <i>Euglypha strigosa</i> (forma glabra).
5.2		<i>Oicomonas termo</i> , <i>Heteromita globosa</i> , <i>H. lens</i> , <i>Cercomonas</i> sp., <i>Phalansterium solitarium</i> , <i>Spiromonas angusta</i> , <i>Petalomonas angusta</i> , <i>Allantion tachyploon</i> , <i>Anisomonas minus</i> .	<i>Cyclidium glaucoma</i> and 2 unidentified species.	<i>Dimastigamoeba gruberi</i> , <i>A. radiosa</i> , <i>Actinophrys</i> sp., <i>A. diploidea</i> , <i>Trinema lineare</i> , <i>Diffugia constricta</i> , <i>Euglypha laevis</i> , <i>Assulina muscorum</i> .

## APPENDIX.

## NOTES ON THE SPECIES FOUND.

1. *Flagellata*.

*Cercomonas*.—This is one of the commonest of soil Flagellates. The usual species is *C. crassicauda* Alexoieff, but the specific characters are not very well defined, and other species such as *C. longicauda* may also have been present in some of the cultures.

*Heteromita*.—This genus is extremely abundant in all soils, commonly occurring in two forms which agree closely with the description of *H. lens* Müller and *H. globosa* Stein (see especially 35). The former is a small organism, lenticular in shape and from  $4\mu$  to  $6\mu$  in length, though sometimes very small globular individuals occur only  $2\mu$  or  $3\mu$  in diameter. A pair of flagella arise at the anterior end, one directed forwards being about twice the body-length, and the other, which is normally trailed passively, being a little longer. The nucleus is not visible in the living animal, and the contractile vacuole is also not usually apparent, but when present lies just behind the middle. When swimming the body is turned at a sharp angle to the direction of motion, and the anterior flagellum lashes vigorously through a wide amplitude. At times the tip of the flagellum adheres to the glass slide, and both flagella wave actively, so that the animal jerks vigorously from side to side without progressing. When stained with hæmatoxylin a typical vesicular nucleus appears surrounded by a dense mass of peripheral chromatin, especially at the posterior side. The cyst is small (diameter about  $4\mu$ ), thin-walled, and usually homogeneous in structure, though sometimes the protoplasm appears concentrated round the wall, leaving a vacuole in the centre, to one side of which there may be a small refractile granule.

*Heteromita globosa* is larger (length  $8\mu$  to  $12\mu$ ), and more variable in shape. Usually the anterior end is rounded and the posterior end slightly narrower, but sometimes this is reversed. At times the protoplasm becomes quite plastic at the posterior end, which may then adhere to the glass slide while the anterior part moves round slowly in circles owing to the movements of the anterior flagellum. In this condition the hinder part may become drawn out into a long filament before the animal breaks free. The flagella arise together just behind the anterior extremity, the shorter one being about equal to the body-length and directed forwards, while the other, which is usually trailed passively, is about  $1\frac{1}{2}$  times as long. A nucleus is clearly visible near the anterior end, and when stained shows much less peripheral chromatin than in *H. lens*. The contractile vacuole is central. The movements of the body are vibratory; it is not turned outwards so sharply as in *H. lens*, and the anterior flagellum lashes through a smaller amplitude. The cyst has a thin outer wall which is usually raised a little from the thicker inner wall. The protoplasm of the cyst is hyaline, and contains a large very refractile granule against which is a big vacuole. This

cyst is well figured by Puschkarew (27), but the two walls are always separable, and the granule and vacuole are sometimes poorly developed or even absent.

Though these two species seem quite distinct, apparently intermediate forms both of the active and encysted stages are frequently found, the identification of which is very difficult, and in cultures of either species a few abnormally large or small individuals are usually found which might be mistaken for members of the other species. Until conclusive observations in pure cultures have been carried out, there consequently remains a doubt whether we are actually dealing with two true species or with two extreme forms of a single very variable species.

SAINOURON MIKROTERON\* (n. gen., n. sp.). (Pl. 24. figs. 1-6.)

A brief description of this organism under the name of Sp.  $\gamma$  has already been published (12). It is a small flagellate from  $3\mu$  to  $6\mu$  in length with a single flagellum, slightly longer than the body, which arises just behind the anterior end and is directed backwards. The anterior end is rounded, and usually the body is slightly crescent-shaped (fig. 2) (the side from which the flagellum arises being slightly concave) and tapers somewhat towards the posterior end. In these specimens the maximum width is about half the length or less, but sometimes individuals occur in which the posterior end is swollen, and the side from which the flagellum arises is sigmoid in outline, the concavity being limited to the anterior end. In normal cultures the shape is quite persistent, but in the deeper parts of hanging-drop cultures plastic individuals sometimes occur adhering to the glass slides (figs. 4, 5). The plastic individuals contain ingested bacteria, which are absent in the normal free-swimming form, the nutrition of the latter being apparently wholly saprophytic. The nucleus is not visible in the living animal, probably owing to its small size, and no contractile vacuole has ever been observed.

The movements are very like those of a small *Heteromita*, since the flagellum is trailed quite passively while the animal progresses at a considerable speed with a rapid vibratory motion, the body being turned at an angle of about  $20^\circ$  to the direction of motion. The progression is in a straight line (not spiral), and the animal does not turn on its axis as do most organisms which possess an anterior flagellum.

When stained, a large vesicular nucleus becomes visible in the anterior part. The basal granule varies considerably in size and position, at times lying against the anterior side of the nuclear membrane and at other times being quite free from it and apparently not connected to it by any rhizoplast. Most characteristic of this species, however, is a large mass of plastin, often visible in the living animal as a refringent body, which lies just behind the nucleus or at times forms a ring completely enclosing it (figs. 1-3). In a dividing animal this body divides immediately after

\* *trains*, to wag.



the basal granule, but its size and shape seem to depend on the general metabolism of the organism rather than on the phase of its life-cycle, for dividing specimens can be found in which two nuclei are present, each entirely surrounded by a ring of plastin, whereas in other cases the plastin divides to form two centrally-placed spherical masses. The changes which this mass undergoes have unfortunately up to the present obscured the division changes of the karyosome, the difficulty of observing which is rendered greater both by the extremely small size of the organism and by the fact that the karyosome itself varies considerably in size and at times appears to be entirely lost (fig. 3), as in the case of *Herpetomonas* (*Leptomonas*) *jaculans* as described by Berliner (7).

In old cultures thin-walled spherical cysts rarely reaching as much as  $3\mu$  in diameter appear (fig. 6). The protoplasm is uniform and shows no characteristic features, but tends to be denser round the periphery of the cyst and vacuolated in the centre. Staining reveals a simple excentrically-situated nucleus, the mass of plastin apparently having been lost before encystment.

This species is very widely distributed. It is common in the Rothamsted soil, and has also been found in samples of soil from Africa, the West Indies, Azores, etc.

*SAINOURON OXU* (n. sp.). (Pl. 24. figs. 7-10.)

This species resembles the foregoing very closely. It is, however, considerably larger, being from  $10\mu$  or  $12\mu$  in length in a young culture, but diminishing to  $6\mu$  or  $7\mu$  in old cultures. The anterior end, instead of being rounded, is generally drawn out into a curved beak, at the base of which the flagellum arises (fig. 7). This beak is occasionally bent or flattened (fig. 8), and the whole body is in fact more plastic than in *S. mikroteron*. A large vesicular nucleus lies in the anterior part of the body, and is generally surrounded by a complete peripheral ring of chromatin (fig. 8), but frequently the ring is broken and in its place one or more deeply-staining masses (recalling the plastin masses of *S. mikroteron*) lie against the posterior part of the nuclear membrane (fig. 7). The basal granule from which the flagellum arises is situated at the base of the beak when the latter is present, or slightly to one side of the anterior extremity when the beak is not present. Usually the granule lies too close against the nuclear membrane to be distinguishable (fig. 9), but at times there is a considerable space between them (figs. 7, 8). In spite of careful examinations of cultures of all ages, no contractile vacuole has been found. Nutrition appears to be saprophytic as in *S. mikroteron*, which species *S. oxu* also resembles very closely in its movements. It shows, however, one interesting peculiarity in its behaviour in that when a drop of a culture is put on a slide and covered with a coverslip for examination, the organisms remain perfectly quiescent for some time. The first signs of activity usually appear about one minute after the preparation of the slide,

but even after four minutes there are usually still a considerable number that have not resumed their movements.

The cysts (fig. 10) are thin-walled, spherical, and from  $4\mu$  to  $5\mu$  in diameter. The contents are granular, the granules usually being arranged in a ring. When stained, a nucleus with karyosome and peripheral blocks much as in the active stages is visible.

It has not been found outside Spitsbergen, where it occurred in two samples of moss, both from Klaas Billen Bay.

*ALLANTION TACHYPLOON* \* (n. gen., n. sp.). (Pl. 24. figs. 11, 12.)

This organism, though it resembles *Sainoureon* in having a single flagellum which arises just behind the anterior end and is directed backwards, has such a characteristic mode of progression that one feels constrained to create a new genus for it. In size it varies from  $7\mu$  to  $14\mu$  (usually  $8\mu$ – $10\mu$ ), and the width is about half the length. The shape is very constant, being equally rounded at the two ends and usually slightly crescentic. It is enclosed in a firm pellicle, and no trace of pseudopodia can ever be found; in fact, the only deviations from the typical shape are the occurrence of shortened, almost spherical individuals, or of organisms which have their concave side (*i. e.* the side from which the flagellum arises) compressed, appearing in consequence more transparent than the rest of the organism when they are seen in side view, and causing the animals to become triangular in cross-section instead of circular, as is more normal. Both these forms are commonest in rather old cultures. There is a simple vesicular nucleus with some peripheral chromatin in the anterior half of the body, and one or more deeply-staining spherical masses, presumably metabolic products of some kind, are often found in various parts of the body behind the nucleus. There is no contractile vacuole. The flagellum is about half as long again as the body, and is very much stouter than in such flagellates as *Sainoureon* or *Heteromita*. It is invariably directed backwards. When the animal is progressing, the flagellum is applied for its whole length to the substratum, while the body itself is turned upwards at a sharp angle. Neither the flagellum nor the body of the animal shows any trace of vibration or movement of any kind, and yet the animal glides rapidly forwards, covering a distance of two or three times its own length per second. The organism whose movements resemble this most nearly is *Helkesimastix* Woodcock & Lapage (36), from which the present species differs in being quite without an anterior flagellum (the presence of which in *Helkesimastix* I have been able to confirm, but which plays no appreciable part in the animal's locomotion). It also differs in the absence of a contractile vacuole, and in the presence of a firm pellicle as a result of which the flagellum is quite free except at its point of insertion instead of adhering to the body as it does in *Helkesimastix*. This mode of progression, depending presumably on some surface action

\* ἀλλαντιον, a little sausage; ταχηνπλοον, swiftly-sailing.

between the flagellum and the surface to which it is applied, may however occur in other organisms having what has so far been regarded as a passive trailing flagellum. It is impossible, for instance, to watch a *Cercomonas* for long without concluding that its characteristic gliding motion is not produced by the tractellar action of the anterior flagellum, for the motion continues without a break even when this flagellum is temporarily motionless or recovering from its stroke; and, further, the mean position of the flagellum often forms a wide angle with the direction of motion of the organism, which, on the other hand, is always in a line with the posterior flagellum. The movements of *Cercomonas* and *Helkesimastix* are in fact so similar (in a casual examination it is easy to mistake *Helkesimastix* for a small *Cercomonas*) that it seems probable that they are both produced in the same way and that the motive power in both, as in *Allantion tachyploon*, is really the so-called trailing flagellum.

When *Allantion* is not moving in this way, it adheres by the tip of the flagellum to the slide and jerks violently from side to side without progressing as a result of repeated flexions and extensions of the flagellum.

Remains of ingested bacteria are sometimes found, so that nutrition is apparently holozoic though the actual method of feeding has not been observed. No cysts of this species have been identified.

Though this organism does not appear to have been described before, it occurs very commonly in soils both from Europe and from the tropics.

*ANISONEMA MINUS* (n. sp.). (Pl. 24. fig. 13.)

This species is quite typical of the genus in all except size. It is usually from  $6\mu$  to  $7\mu$  in length and never exceeds  $9\mu$ , whereas the lowest limit for any *Anisonema* given by Senn (30) is  $11\mu$ . It is strongly flattened and has a longitudinal groove on the under side. In outline it is egg-shaped, but slightly asymmetrical at the anterior end. The anterior flagellum is stout and about equal to the body-length, while the posterior flagellum is rather more slender and about twice as long. They arise from separate basal granules a little way behind the anterior end. The contractile vacuole is central, but a pharynx has not been definitely discerned. There is a large elliptical vesicular nucleus lying to one side of the body, containing a karyosome, which though usually spherical is sometimes irregular in shape, and a ring of peripheral chromatin. The movements are slow and very steady, being produced by the movements of the anterior flagellum, which lashes through a wide amplitude.

This species occurred in one sample only. I have, however, found it in soils from the West Indies, so that although apparently never abundant, it seems to be a widely-distributed soil form.

*Cladomonas* sp.—This occurred in only one culture from soil sample 5 (1921). The monads are spherical to ellipsoidal in shape, from  $5\mu$  to  $7\mu$  in length, and with two forwardly-directed flagella, each about  $1\frac{1}{2}$  to  $1\frac{3}{4}$  times the

body-length, inserted at the anterior end. Each monad is situated at the end of a tube usually with only the flagella projecting, but sometimes the cell itself protrudes to some extent. The tube is colourless and transparent, and is quite empty except for the organism at its tip; in fact, but for the cocci adhering to it, it would easily pass unnoticed. Its composition was not investigated, but it is flexible and yields to the movements of the organism. Occasionally one finds an unbranched piece of tube,  $50\mu$  or more in length, with a single flagellate at its end, but more usually the tube branches, though not with the regular dichotomy of *C. fruticosa* Stein. Usually, however, the distal parts of the tube are surrounded with a dense mass of bacteria, protozoal cysts, etc., so that its ramifications cannot be fully followed out. The flagella are held at an angle of about  $20^\circ$  to one another and vibrate rigidly without bending. These movements are so rapid that the flagella can then only be detected by the characteristic movements of the surrounding bacteria, etc., one or two of which usually adhere to the tip of each flagellum, and are seen to be whirling round in a small circle. Occasionally the motion stops, and the animal remains at rest for a few seconds. The effect of the whirling of the flagella is to drive small bacteria towards the mouth of the tube, where they adhere both to the walls of the tube itself and to the body of the animal, which is consequently always the centre of a small mass of the organisms. Occasionally a single monad is found adhering to the glass slide without any tube. In this condition the flagella vibrate just as usual, causing cocci to come against the body, to which they then adhere.

This organism differs from *C. fruticosa* Stein only in the less regular branching of the tube, a feature which hardly justifies the creation of a new specific name.

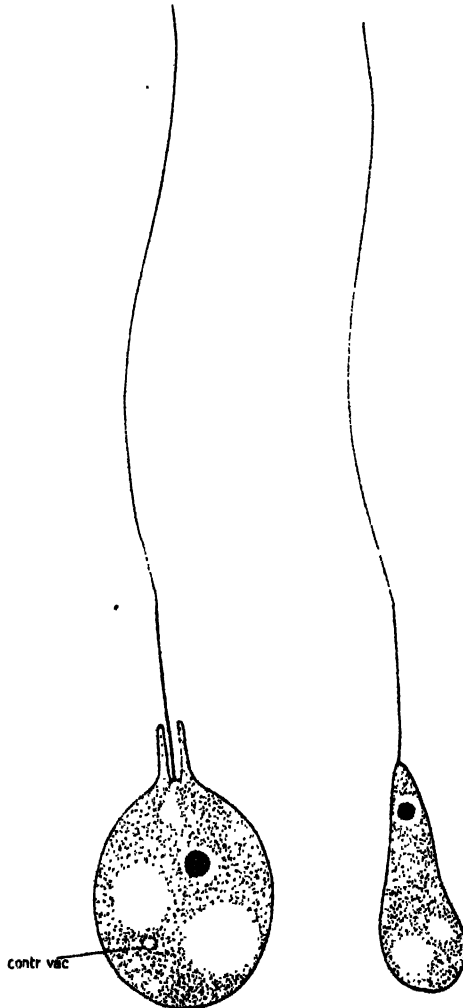
*PHALANSTERIUM SOLITARIUM* (n. sp.). (Pl. 24. figs. 14, 15 & text-figs. 1, 2.)

This organism differs in several respects from the two established species *P. consociatum* Fresenius and *P. digitatum* Stein. It usually appears in cultures in the form of free-swimming monads  $10\mu$  to  $15\mu$  in length (text-fig. 1) and more or less spherical in shape, though sometimes rather elongated, and often distorted by the presence of large vacuoles. At the anterior end is a single flagellum, three or four times as long as the body, which is surrounded at its base by a narrow "collar," into which a cytopharynx opens. The flagellum is very characteristic, the proximal part (about one-fourth of the whole length) being stout and fairly rigid, while the distal part tapers to a very fine and flexible whip. Unlike the flagellum of the Craspedomonads, which is always a pulsillum, this flagellum acts as a tractellum, so that the creature swims with its collar directed forwards. A reversal of this mode of swimming has never been observed. The mode of swimming enables the species to be easily recognised, since the whole organism vibrates rapidly as it were about a pivot situated near the hinder end of the body. Often a few cocci adhere to the rigid part of the flagellum,

and these are consequently seen vibrating vigorously a short distance in front of the animal itself. The progression is rapid and in a straight line without any tendency on the part of the organism to turn on its axis. It follows that the movement of the flagellum (which is too rapid to be

FIG. 1.

FIG. 2.



*Phalansterium solitarium*,  $\times 2500$ .

1. Normal living form with collar.
2. Elongated form from an old culture.

visible) must consist of a lashing from side to side, and is not the typical spiral movement of the *Craspedomonads*. The contractile vacuole is not usually visible, but is situated just behind the centre of the body.

In old cultures the organisms often lose their spherical shape and become very narrow, tapering particularly at the anterior end (text-fig. 2). In this condition the collar is difficult to observe, and often appears to be completely merged in the cell protoplasm. Even in the more typical spherical form the collar is occasionally invisible, and at death it is invariably completely retracted.

In the living organisms the nucleus, when it is visible, is composed of a single spherical karyosome surrounded by a narrow clear zone. Unfortunately it has only been possible to obtain a single stained preparation in which the karyosome was often vacuolated (Pl. 24. fig. 14) or distorted by the pressure of large cytoplasmic vacuoles (Pl. 24. fig. 15). The fixation of these specimens appeared to be satisfactory, but until further preparations have been obtained, it is impossible to say whether or not these appearances are abnormal.

In its sedentary phase the organism becomes surrounded by a thick gelatinous layer. Unlike *P. consociatum* and *P. digitatum* it does not form any definite colonies, though frequently a number of these gelatinous capsules are formed side by side. Frequently also two or more cells occur in a single capsule, but the process of multiplication has not been observed. The flagellum projects through the wall of the capsule, which has no well-defined opening, and its fine whip-like distal portion lashes vigorously with a spiral movement, which causes cocci etc. to be whirled towards its base, where they accumulate in a mass which quivers slightly with the movements of the flagellum. The whole gelatinous capsule, in fact, becomes encrusted with cocci etc. so that the details of the organism inside are not easily distinguished. The collar appears to be rather smaller than in the free-swimming form, and may frequently be entirely lost. Neither in the sessile nor in the free-swimming phases have any bacteria been observed inside the collar, and the mode of nutrition is therefore unknown. While in this gelatinous capsule, the organism loses its collar and flagellum and becomes enclosed in a thick wall, forming a rather angular cyst, which, however, has none of the ridges shown in Cienkowski's figure (11).

This species has also been found in soils from Rothamsted and from the West Indies.

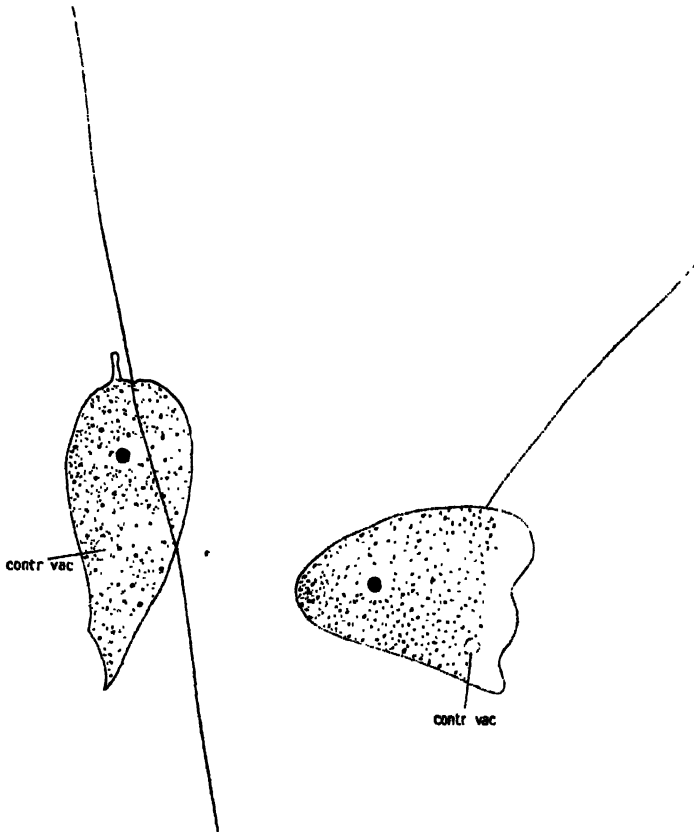
Of the other flagellates recorded, *Oicomonas termo* Ehrenb. is one of the most numerous and most ubiquitous soil organisms. *Spiromonas angusta* (Duj.) Kent, *Helkesimastix fecicola* Woodcock & Lapage, and *Phyllomitus* sp., though much less abundant, are not uncommon in soils from other regions. *Petalomonas angusta* (Klebs) Lemm., found in soil sample 3 (1922), does not seem to have been found in the soil before, though the nearly related *Copromonas subtilis* Dobell is not uncommon.

There were in addition a small number of unfamiliar forms which appeared in one or more of the cultures, but in such small numbers that a satisfactory

examination was not practicable, and the attempts to obtain stronger sub-cultures failed. It is possible that some of these may have been new species. Of these forms the following two deserve mention, since they have each been found in one or more other localities; and although it has not so far been possible to obtain the stained preparations necessary for an adequate description, the appearance of the living organisms is quite

FIG. 3.

FIG 4.



Sp.  $\delta$ ,  $\times 2500$ ; freehand drawings from life.

3. Free-swimming form with anterior pseudopodium.
4. Amoeboid form.

characteristic. It is hoped that a satisfactory identification or description may be published later.

#### Sp. $\delta$ . (Text-figs. 3, 4.)

In the flagellate condition (text-fig. 3) this organism is very plastic, and its shape is therefore rather indefinable, but typically the anterior end is rounded, and posterior end tapers to a point. Quite spherical individuals,

however, are not uncommon. Finger-like pseudopodia may be formed at all parts of the body, but they are commonest at the posterior end. Two flagella arise in a slight pit at the anterior end, of which one is directed forwards and is between 1 and  $1\frac{1}{2}$  times the length of the animal, and the other, which is a little longer, is directed backwards or slightly to one side, but is quite free from the body except at its point of insertion, thus differing from the corresponding flagellum in *Cercomonas*. In small specimens the relative lengths of the flagella are often greater, up to three times the body-length. A vesicular nucleus is usually clearly visible in living specimens at or just in front of the middle of the organism, and a single contractile vacuole can occasionally be observed near the hinder end. The usual length is about  $15\mu$ , though occasionally small specimens of  $6\mu$  to  $10\mu$  occur. The movements are usually jerky, both the flagella being held more rigidly than in most flagellates, the anterior one vibrating vigorously.

The amoeboid stage (text-fig. 4) is less commonly observed. One flagellum is retained which is directed sideways and continues to vibrate vigorously while the animal moves forward with a single broad pseudopodium, the posterior end being rounded. As in the swimming stage, the nucleus is more or less centrally placed and is easily visible, but the contractile vacuole now lies anteriorly between the ecto- and ento-plasms.

This species resembles the genera *Cercobodo* Krassilstchik and *Dimastigamoeba* Blochmann rather closely in many respects. From the former, however, it is distinguished by the true amoeboid movements of the sessile form, while the fine radiating pseudopodia which Blochmann mentions as being sometimes formed by *Dimastigamoeba* have not been observed.

It occurred in only one of the present soil samples, but has been found on several occasions in small numbers in soil from Harpenden and from the Azores, W. Indies, and other localities.

#### Sp. e. (Text-figs. 5, 6.)

In its general appearance and movements this organism is somewhat like *Allantion tachyploon* (see p. 461). The length is usually about  $18\mu$ , though individuals as small as  $10\mu$  or as large as  $24\mu$  occasionally occur. The width is about half the length. The sides are straight and the ends both rounded. In section it is circular or slightly flattened "dorso-ventrally." The shape is persistent and the body not flexible, but finger-like pseudopodia may occur at either end. These are usually about  $4\mu$  to  $6\mu$  long, but occasionally a much longer one is formed. A stout flagellum, slightly longer than the body, arises at the extreme anterior end, and is directed backwards as in *Allantion*. In most individuals a very short second flagellum, about  $2\mu$  to  $3\mu$  in length, can be detected. Near the base of the flagella are two prominent contractile vacuoles, but the nucleus is usually indistinguishable in the living organism, and, as already mentioned, no



observations of its cytology have been made. The hind end of the body often contains a considerable number of granules, apparently the remains of food, though the actual ingestion of bacteria has not been observed. The movements are very similar to those of *Allantion*, the long flagellum being applied closely to the glass slide, and the whole animal gliding quickly and steadily forwards. When the short second flagellum was visible it moved vigorously from side to side, but its movements were not sufficiently powerful to impart any vibration to the animal as a whole. The characteristic quiescence in a newly-prepared slide, noted in the case of *Sainouron oxu* (p. 460), is shown to an even more marked degree by this species, as much as ten minutes sometimes elapsing before movements are resumed. If the drop of culture fluid is spread out on a slide but not covered with a cover-slip, activity recommences much more quickly

FIG. 5.

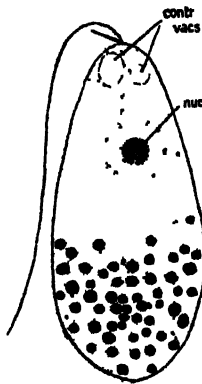


FIG. 6



Sp. c.

## 2. Ciliata.

None of these require any comment except *Uronema* sp., which was found in soil sample 5 (1921). The numerous specimens found appeared identical with those obtained in cultures of sea-weeds from Plymouth, and it is possible that they were really marine organisms introduced into the soil in the droppings of sea-birds. Unfortunately at the time I was not aware of Schewiakoff's and Buddenbrock's (8) work on this genus, and not having made drawings, cannot say whether the organisms found were *U. marinum* Duj. or the very similar species *U. schewiakoffi* Buddenbrock, which appears to be a true fresh-water form.

## 3. Rhizopoda.

*Amoeba limax*.—The identification of the different species of "limax" amoebae is usually only practicable when the complete life-history is known, or at least when both the active and the encysted stages are available. In the

cultures in which only active individuals could be found the identification is consequently incomplete. The common soil species *Nagleria (Dimastigamaba) gruberi* (Schardinger) Alexeieff was found in two of the soil samples, and the very similar form *Hartmanella hyalina* Alexeieff in three of the mosses. A characteristic small species described in a recent paper (12) as sp. *a* also occurred in one of the moss samples. Unfortunately this organism does not grow very well in cultures, and consequently it is still impossible to complete the description of it, or to name it satisfactorily.

*Amæba limicola* Rhumbler.—This species occurred in only one culture and was smaller than usual, being only about  $20\mu$  in diameter when rounded.

*Amæba respertilio* Penard.—Penard records this species as being present "en assez grand abondance" in his Spitsbergen material, but in the present investigation it was found in only one moss sample. The specimens examined were nearly all in the radiate form when first observed, but passed over into the more active non-radiate form when transferred to a slide for closer examination. In the latter condition the average length was about  $60\mu$ .

One sample of moss from Prince Charles Foreland gave a few specimens of a smaller amæba which may belong to this species. When active this animal is constantly and rapidly changing its shape, but does not progress. The pseudopodia are numerous and are of two kinds—narrow finger-like ones reaching about  $20\mu$  in length, and other very fine ones which are even longer. At times the amæbæ become rounded and motionless, with very short finger-like pseudopodia projecting all over the body. The diameter is then from  $18\mu$  to  $30\mu$ . There is apparently only one contractile vacuole, which is situated near the middle of the body and at times reaches a very considerable size.

*Amæba terricola* Greef occurred in three soil samples and in one moss. They were all perfectly typical except in size, in which respect they mostly agreed with those found by Penard. The specimens from the mosses were usually about  $50\mu$  in diameter and those from the soils even smaller ( $20\mu$ ). Soil sample 4 (1922) contained a few full-sized ones of  $120\mu$  in diameter, with a nucleus of  $35\mu \times 18\mu$  and a contractile vacuole which at times reached a diameter of  $50\mu$ . Though encystment is unknown in the European members of this species, it apparently does sometimes occur, for the specimens found in the material brought back by the British Antarctic Expedition of 1907–1909 were all encysted (25). No cysts were found, however, in the material.

*Amæba striata* Penard.—This beautiful amæba occurred in its typical form in one of the moss samples. When progressing steadily its dimensions were about  $60\mu$  by  $36\mu$ . The large contractile vacuole (diameter  $12\mu$ ) is characteristic of the species, but in the present case it was almost invariably single. Once only was it observed being formed by the coalescence of three smaller vacuoles.

A single small specimen (length  $30\mu$ ) was found in another sample from the same locality.

*Amœba actinophora* Auerb.—This organism, as it appeared in the cultures, agreed closely with the figures and description of *A. actinophora* given by Cash, but the envelope was much less well defined than in those figured by Penard (22) under the name of *Cochliopodium actinophorum*. The usual appearance is of a small granular amœba completely surrounded by a wide ectoplasmal border except during the extrusion of faecal matter, when the granular endoplasm extends to the surface at the hinder end. In this condition it changes shape quickly or moves forward slowly, the appearance being somewhat like that of a broad limax except for the wide clear border of ectoplasm. The anterior end is wider than the posterior, and the contractile vacuole is anterior. At other times progression ceases, and long, pointed pseudopodia arise from the endoplasm, which projects right through the ectoplasm. The length of the amœba varies from  $24\ \mu$  to  $36\ \mu$ , and the pseudopodia may reach about  $15\ \mu$  in length.

*Corycia flava* Greef.—Though empty, rolled-up tests probably belonging to this species were observed in many of the moss samples, living specimens occurred in only two (one from each locality). They were quite typical and the size was about  $135\ \mu$ .

Several specimens of *Corycia coronata* var. *simplex* (Penard), which is now generally regarded as a variety of *C. flava* (32), occurred in one of the other samples from Klaas Billen Bay. Diameter of shell  $105\ \mu$  to  $120\ \mu$ .

*Diffugia*.—As in Scourfield's and Penard's samples. *D. constricta* Ehrenb. was much the commonest testaceous rhizopod found. The numerous specimens recorded as *D. globulus* Duj. were all empty tests, and it is therefore impossible to be sure whether they belonged to this species or to the genus *Phryganella* Penard, as the two are distinguishable only by the form of the pseudopodia. The diameter was usually between  $33\ \mu$  and  $50\ \mu$ , but in one sample very large specimens (diameter  $120\ \mu$ ) were found which were more probably tests of *Phryganella nitulus* Penard. *D. fallax* Penard was also very common. The size was generally about  $60\ \mu$  in length by  $54\ \mu$  in greatest width, with an aperture of between  $25\ \mu$  and  $30\ \mu$ . The smallest individual recorded was  $30\ \mu$  long and the largest  $72\ \mu$ .

*D. lucida* Penard, the scarcest of the *Diffugias* found, occurred in only one sample. The size was usually about  $54\ \mu$  in length by  $27\ \mu$  in greatest width. One specimen reached a length of  $80\ \mu$ .

*D. pyriformis* Perty was not common, and varied from  $87\ \mu$  to  $105\ \mu$  in length.

*Centropyxis*.—Although the two species of this genus were about equally widely distributed among the samples, the individuals of *C. laevigata* Penard were considerably the more numerous. They were mostly rather small specimens, the diameter of the shell usually lying between  $60\ \mu$  and  $80\ \mu$ , with a height of  $45\ \mu$  to  $60\ \mu$  and an aperture of from  $25\ \mu$  to  $45\ \mu$  in diameter. A single very large specimen ( $144\ \mu$  in diameter and  $72\ \mu$  in height) was

found which differed from the smaller ones in having a transparent yellowish-brown chitinous test free from sand-particles.

The specimens of *C. aculeata* Stein were also on the average slightly smaller than usual, varying from  $85\mu$  to  $120\mu$  in diameter and with apertures of from  $20\mu$  to  $38\mu$ . This species showed considerable variation in form. The commonest type agrees closely with Cash's var. *spinosa*, as the spines were relatively long and the mouth distinctly lobed. This type included the largest specimens found (diameter  $114\mu$  to  $120\mu$ ). In others the mouth was circular and the spines very short, often in fact reduced to mere knobs. The smallest specimens found, those with a diameter of from  $85\mu$  to  $95\mu$ , were almost invariably spineless, and no doubt belong to the *C. aculeata* var. *ecornis* of Leidy.

*Arcella*.—Typical tests of *A. arenaria* Greef varying in diameter from  $72\mu$  to  $180\mu$  were by no means uncommon. The tests of *A. vulgaris* Ehrenb., though clearly differentiated from the others by the perfectly regular domed appearance without any border when seen in side view, were decidedly larger than usual, being between  $100\mu$  and  $190\mu$  in diameter.

*Hyalosphenia minuta* Cash.—A very few specimens of this species were found in one of the soils. Average dimensions: length  $34\mu$ , greatest breadth  $20\mu$ , mouth  $10\mu$ .

*Nebela collaris* Leidy.—Length  $84\mu$  to  $135\mu$ , greatest width  $48\mu$  to  $72\mu$ , aperture  $18\mu$  to  $30\mu$ . A broken test was also found which apparently belonged to this species, and which when complete must have attained a length of about  $160\mu$ . In structure the tests all resembled that figured by Leidy (pl. xxiv. fig. 11). Scourfield also found some pitted like *Hyalosphenia* or like Leidy's pl. xxiv. fig. 12.

*Nebela lageniformis* Penard.—This is described by Cash (10) as a definitely sub-alpine species. Typical but rather small specimens were found in one of the soil samples, the dimensions being: length  $103\mu$  to  $105\mu$ , breadth  $48\mu$  to  $54\mu$ , aperture  $21\mu$  to  $25\mu$ , length of neck  $33\mu$  to  $36\mu$ .

*Quadrula irregularis* Archer.—This species was abundant in most of the mosses from Kluas Billen Bay, and showed considerable variation both in size and shape. They mostly belonged to the variety *globulosa* Penard, and had a diameter of from  $25\mu$  to  $45\mu$  and an aperture of from  $9\mu$  to  $15\mu$ . But several were more elongated and frequently not quite symmetrical, belonging therefore to Penard's variety *oblonga*.

*Euglypha*.—The specimens found were all typical and require little comment.

*E. ciliata* Ehrenb. was the commonest species in the mosses from Kluas Billen Bay, and varied from  $70\mu$  to  $90\mu$  in length and from  $51\mu$  to  $60\mu$  in greatest width.

*E. strigosa* Leidy was also common. Most of the specimens belonged to the variety *glabra* Wailes, and varied in length from  $63\mu$  to  $96\mu$ , in greatest

width from  $38\mu$  to  $66\mu$ , and with apertures between  $15\mu$  and  $24\mu$  wide. Two ciliated specimens only were found with the dimensions: length  $56\mu$  and  $65\mu$ , greatest width  $33\mu$  and  $43\mu$ , and apertures  $15\mu$  and  $31\mu$ .

*E. tuberculata* Duj. occurred in one sample only. The dimensions were: length  $56\mu$ , greatest width  $27\mu$ , aperture  $12\mu$ , body-scales (elliptical)  $7\mu$  long. This is no doubt the *E. alveolata* found by Penard and Scourfield.

*E. laevis* Perty.—This species was not at all common and most of the specimens found were damaged, so that the identification was in many cases not very satisfactory. The dimensions of those found in the mosses were: length  $39\mu$  to  $60\mu$ , greatest width  $24\mu$  to  $40\mu$ , and aperture  $11\mu$  to  $15\mu$ . The specimens found in the soils were smaller, some being only  $18\mu$  long.

*Assulina muscorum* Greef (*A. minor* Penard and *A. seminulum* (pars) Leidy).—Typical specimens varying from  $45\mu$  to  $54\mu$  in length were abundant in two of the moss samples from Prince Charles Foreland; in fact, their presence constituted the most striking difference between these mosses and those from the other locality. They were also quite numerous in some of the soils, but these specimens were rather more variable in size (length  $33\mu$  to  $53\mu$ ) and in shape, which was frequently asymmetrical. The soil specimens were also quite colourless, but as they were all dead it was impossible to decide whether this was due to the usual brown membrane having been destroyed by the soil solution or whether they really belonged to a colourless variety.

*Cyphoderia ampulla* var. *nitra* Wailes.—Only a few individuals of this species were found, and in most cases it was impossible to distinguish the structure of the test, which appeared quite homogeneous. In one case, however, regular polygonal scales could be detected. The specimens were uniformly small, the length varying from  $50\mu$  to  $56\mu$  instead of the normal  $100\mu$  to  $120\mu$  (22), with a greatest width of  $25\mu$  to  $27\mu$  and an aperture of  $10\mu$  to  $12\mu$ . The usual yellowish tint was also absent and the tests (which were all empty) were perfectly colourless.

In each of three moss samples a single specimen of a larger yellowish retort-shaped test was found. Two of these measured  $75\mu$  in length and the third was nearly  $170\mu$ . These tests showed no trace of any structure and were all flexible, being in fact dented and creased when found. The section appeared to be circular, but it was impossible to be quite certain of this owing to the damage that they had suffered. They probably belonged to the species *Campascus triqueter* Penard, which is confined elsewhere to lakes of glacial origin and is consequently regarded (24) as a relict of a true arctic fauna. The occurrence therefore of this otherwise lacustrine form in arctic mosses is of particular interest, and it is unfortunate that no undamaged specimens were found.

*Trinema*.—*T. enchelys* Ehrenb. and *T. lineare* Penard were both quite common, though the former species was not recorded from Prince Charles

Foreland. The former varied from  $33\mu$  to  $65\mu$  in length and the latter from  $16\mu$  to  $30\mu$ . *Trinema complanatum* Penard was also common in two of the moss samples from Prince Charles Foreland, and is no doubt the form observed by Scourfield ( $1/400''$  long) which he compares with Leidy (pl. xxxix. figs. 41, 54, 61, 63). They were mostly between  $45\mu$  and  $50\mu$  in length by  $27\mu$  to  $30\mu$  in width, but a few were considerably larger, ranging up to  $75\mu$  long. One sample from Klaas Billen Bay contained, in addition to all these three species, a few large specimens nearly  $70\mu$  in length of *T. enchelys* var. *galeata* Penard, a form very like *T. complanatum*, but distinguished by the presence of lines on the ventral surface curving backwards from the aperture to the sides of the test.

*Corythion dubium* Turanek.—This was very scarce even in the two samples in which it was present. They were mostly from  $40\mu$  to  $50\mu$  in length, but one reached  $65\mu$ .

*Chlamydophrys stercorea* Cienk.—The classification of the *Chlamydophrys* group of rhizopoda has recently been revised by Belar (6), but, as his differentiation is based on the details of nuclear division, it could not be followed here, so the older and wider name *C. stercorea* is therefore retained. Judging from the size (length between  $24\mu$  to  $27\mu$  by  $19\mu$  to  $21\mu$ ), the specimens found probably belong to the species *C. schaudinni* Schussler.

*Nuclearia simplex* Cienk.—The individuals found were all colourless, and appeared identical with those found in English soils.

*Actinophrys* sp.—Only a single specimen was found, and unfortunately a detailed examination was not possible. The diameter was  $21\mu$ . Penard obtained from Spitsbergen a small new species of *Raphidiophrys* (*R. brunii*) of similar dimensions, to which this specimen may have belonged. The two genera are distinguished by the presence of minute spicules in the gelatinous envelope of *Raphidiophrys* which are absent in the case of *Actinophrys*, but as they are not usually visible in the living animal, it is impossible to say whether they were present or not in the specimen found.

#### SUMMARY.

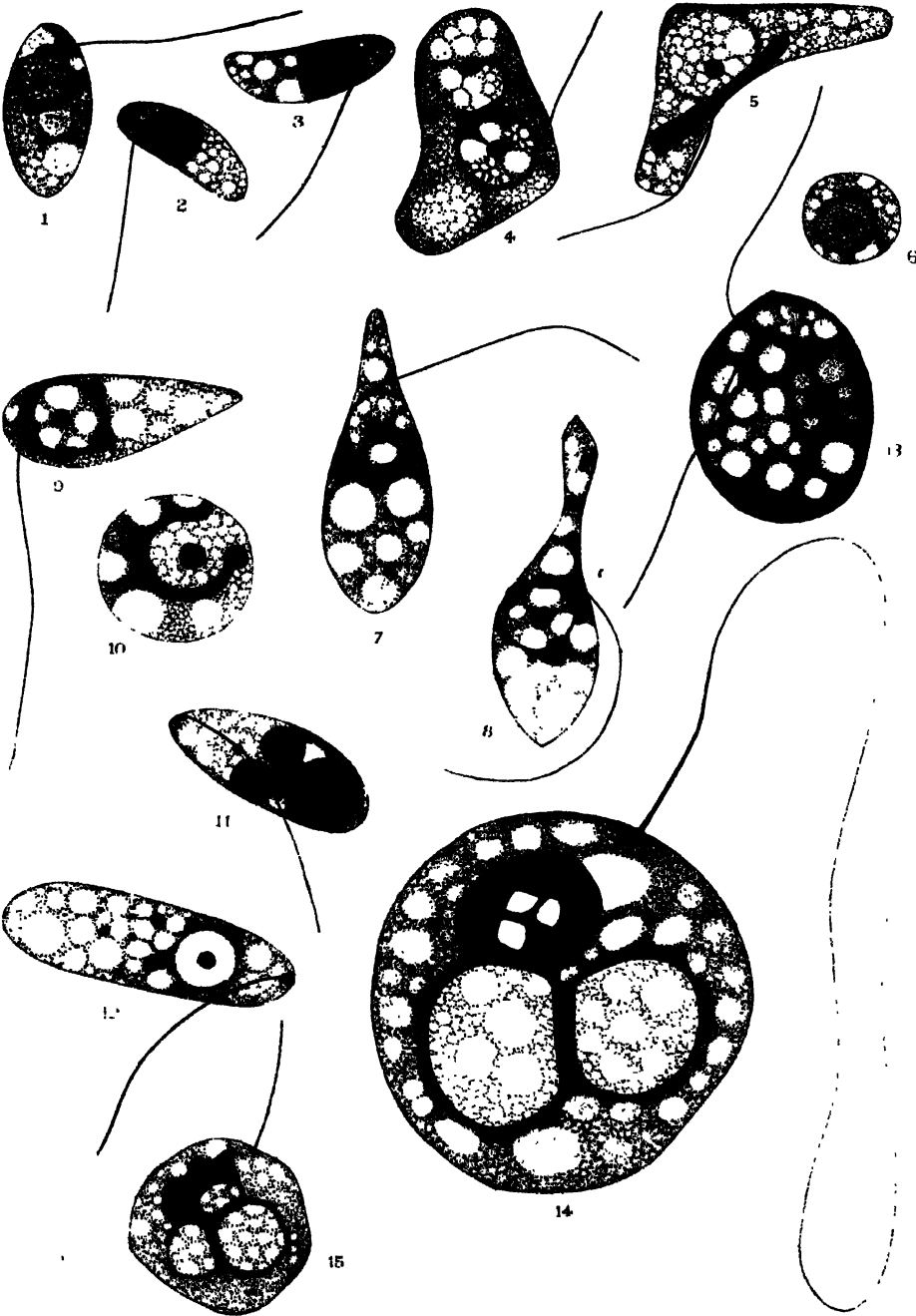
The protozoa contained in 3 samples of mud, 8 samples of soil, and 14 samples of mosses from Spitsbergen have been investigated. An abundant fauna was found, most of which was identical with that occurring in the soils and mosses of temperate lands.

Seven new species of flagellates are described, of which however five have also been found in soils from non-arctic regions.

In conclusion, I wish to thank Mr. G. C. Sawyer for the soil analyses, Mr. E. M. Crowther for the pH estimations, Miss L. M. Crump for suggestions of names for the new species described, and especially Mr. D. W. Cutler, under whose supervision the whole of the work has been carried out.

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## EXPLANATION OF PLATE 24.

All the specimens were fixed in Schaudinn's alcoholic sublimate + 5 per cent. acetic acid and stained in Heidenhain's hæmatoxylin. The figures were drawn with the camera lucida and a Zeiss 1/12" objective and are  $\times 5000$ , except fig. 15 which is  $\times 2500$ .

- Figs. 1-3. *Sainoureon mikroteton*, typical forms.
- 4, 5. " " sessile forms with ingested food bodies.
- Fig. 6. " " cyst.
7. *Sainoureon oru*, typical active form.
8. " " showing plastic beak.
9. " " beak withdrawn.
10. " " cyst.
- Figs. 11, 12. *Allantion tachypleon*.
- Fig. 13. *Anisonema minus*.
- Figs. 14, 15. *Phalansterium solitarium*.

In fig. 15 only the thickened basal part of the flagellum is shown.



On a Collection of Sponges from the Abrolhos Islands, Western Australia.  
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University of London (King's College), and LESLIE M. FREDERICK, M.Sc.,  
Harold Row Student in the Zoological Department, King's College.

(PLATES 25 & 26.)

[Read 21st June, 1923.]

#### INTRODUCTION.

THE collection of Sponges made by Professor Dakin at the Abrolhos Islands is a very rich and, in some respects, a very remarkable one. It comprises 48 determinable species, of which 12 are regarded as new. The collection is especially rich in Calcarea, and includes a number of fine specimens of that extremely rare and interesting sponge *Grantiopsis cylindrica*; a new species of the no less rare and remarkable genus *Lelapia*, and a new genus of Leucascidæ. The Tetraxonida, as usual, form the bulk of the collection, but do not include any very striking novelties; there are, however, two rather remarkable new species of Euceratosa.

The following is a complete list :—

#### Order CALCAREA.

##### Family HOMOCÆLIDÆ.

1. *Leucosolenia grisea* n. sp.
2. *Leucosolenia protogenes* Haeckel.

##### Family LEUCASCIDÆ.

3. *Ascoleucetta compressa* n. gen. et sp.
4. *Leucetta chagosensis* Dendy.
5. *Leucetta microraphis* Haeckel.

##### Family LEUCALTIIDÆ.

6. *Leucaltis clathria* Haeckel.

##### Family SYCETIDÆ.

7. *Sycon gelatinosum* de Blainville.

##### Family HETEROPHIIDÆ.

8. *Vosmaeropsis mackinnoni* n. sp.

##### Family GRANTIIDÆ.

9. *Grantiopsis cylindrica* Dendy.
- 9 a. *Grantiopsis cylindrica* Dendy var. *fruticosa* nov.

## Family LELAPIIDÆ.

10. *Lelapia antiqua* n. sp.

## Order TETRAXONIDA.

## Sub-order HOMONCLEROPHORA.

## Family PLAKINIDÆ.

11. *Dercitopsis minor* Dendy.  
 12. *Dercitopsis mammillaris* (Lendenfeld).

## Sub-order ASTROTETRAXONIDA.

## Family STELLETTIDÆ.

13. *Stelletta brevis* Hentschel.  
 14. *Stelletta debilis* Thiele.  
 15. *Stelletta sigmatriæna* Lendenfeld.  
 16. *Ancorina australiensis* (Carter).  
 17. *Ancorina brevidens* n. sp.  
 18. *Aurora rowi* Dendy.  
 19. *Asteropus simplex* (Carter).

## Family ERYLIDÆ.

20. *Erylus proximus* Dendy.

## Family DONATIIDÆ.

21. *Donatia robusta* (Bowerbank).  
 22. *Donatia multistella* (Lendenfeld).

## Family CHONDROSIDÆ.

23. *Chondrilla australiensis* Carter.

## Sub-order SIGMATOTETRAXONIDA.

## Family HAPLOSCLERIDÆ.

24. *Reniera aqueductus* Schmidt.  
 25. *Reniera cribricutis* Dendy.  
 26. *Reniera permollis* (Bowerbank).  
     *Reniera* spp.  
 27. *Petrosia dura* (Nardo) Vosmaer.  
 28. *Halichondria phakellioides* n. sp.  
 29. *Chalina palmata* (Lamarck).  
     *Chalina* sp.  
     *Pachychalina* sp.  
 30. *Ceraochalina multiformis* var. *manaarensis* Dendy.  
 31. *Phlæodictyon abrolhosensis* n. sp.

## Family DESMACIDONIDÆ.

- 32. *Pseudoesperia carteri* n. sp.
- 33. *Pseudoesperia trichophora* n. sp.
- 34. *Esperella plumosa* Carter.
- 35. *Biemna tubulata* Dendy.
- 36. *Echinodictyum bilamellatum* (Lamarck) Ridley.
- 37. *Anchinoë fictitoides* n. sp.
- 38. *Dendoricella schmidtii* (Ridley).

## Family CLAVULIDÆ.

- 39. *Trachycladus levispirulifer* Carter.
- 40. *Sigmosreptrella fibrosa* Dendy.
- 41. *Spirastrella vagabunda* Ridley.
- 42. *Aaptos aaptos* (Schmidt).
- 43. *Polymastia mammillaris* (O. F. Müller) Bowerbank.

## Order EUCERATOSA.

## Family DARWINELLIDÆ.

- 44. *Megalopastes arenifibrosa* n. sp.

## Family SPONGIIDÆ.

- 45. *Spongelia dakini* n. sp.
- 46. *Psammopemma crassum* Carter var.

## Family SPONGIIDÆ.

- 47. *Hippospongia intestinalis* (Lamarck).
- 48. *Coscinoderma pyriforme* Lendenfeld var.  $\alpha$ .
- 48 a. *Coscinoderma pyriforme* Lendenfeld var.  $\beta$ .

As might be expected from the position of the Abrolhos Islands, the sponge fauna is mainly intermediate in character between that of the more westerly Indian Ocean and that of the more easterly Australian coasts, but it contains a small element apparently derived from the North, viz. *Lelapia antiqua*, nearly related to the Japanese *L. nipponica*; *Stelletta debilis*, previously known only from Ternate, and *Ancorina brevidens*, very closely related to *Ancorina amboinensis* from Amboina; while *Echinodictyum bilamellatum*, though widely spread on the eastern coasts of Australia, seems to be a characteristically tropical or sub-tropical species.

We have to record our indebtedness to Professor W. J. Dakin, D.Sc., for the opportunity of studying this valuable collection; to Mr. M. Burton, M.Sc., for determining the two species of *Donatia*, a genus to which he has devoted special attention; to Mr. Charles Biddolph, the skilled assistant in the Zoological Department of King's College, for the photographic illustrations, and to Mr. J. C. Dendy for help in section-cutting.

1. *LEUCOSOLENIA GRISEA* n. sp. (Pl. 25. fig. 1; Pl. 26. fig. 1.)

There are two specimens in the collection, the larger (R.N. VI. 21), which is attached to a rock by its base, is plicate, consisting of vertical lamellæ which fold and branch in such a way as to lie parallel to one another (Pl. 25. fig. 1). The total height of the specimen is 30 mm., the total width 25 mm., and the average thickness of the lamellæ 1.5 mm. The second specimen (R.N. IV. 3a) consists of a curved lamella, forming an imperfect funnel 20 mm. in height and 10 mm. in diameter at the top.

The surface is smooth, even and sieve-like in appearance, owing to the pseudopores which are thickly and evenly scattered all over it. The oscula, which are marginal in position, are about 1 mm. in diameter and have a slightly prominent margin. Colour in spirit grey; texture firm and compact.

The pseudopores, which are nearly circular and measure about 0.26 mm. in diameter, pierce the pseudoderm, which is about 0.07 mm. in thickness, and lead into wide, irregular interspaces lying between the branching and anastomosing Ascon tubes. The prosopyles are accompanied by groups of black pigment granules which doubtless indicate the porocytes, as in the case of *Leucosolenia coriacea* as described by Minchin [1900], and in that of *Leucosolenia carata* Dendy [1891]; it is the presence of this jet-black pigment which gives the sponge its characteristic grey colour. The granules are not confined to the porocytes, but are also found scattered in the flat epithelium. The secondary Ascon tubes open into the main exhalant canals, which are also lined by basinuclate collared cells, and open to the exterior by true oscula.

The canal system conforms to type B. (Dendy [1891].)

The skeleton consists of triradiate and quadriradiate spicules arranged irregularly in one or more layers in the walls of the Ascon tubes; the triradiates are more densely packed in the thick pseudoderm.

*Spicules*:—(1) Triradiates (Pl. 26. fig. 1a); equiangular; rays measuring about 0.14 mm. by 0.013 mm.; straight, conical, rather bluntly pointed; usually equiradiate, but the basal sometimes a little longer than the oral rays.

(2) Quadriradiates (Pl. 26. fig. 1b); rather scarce, like the triradiates but with the addition of a long, slender, slightly curved and sharply pointed apical ray which projects into the gastral cavity.

This species is readily recognised by its characteristic external form and its grey colour, due to the black pigment granules.

*Register Nos. and Localities*. IV. 3a, Wooded Isle; VI. 21, Sandy Isle.

2. *LEUCOSOLENIA PROTOGENES* Haeckel. (Pl. 25. fig. 2.)

(For discussion and synonymy *vide* Dendy [1891].)

There is in the collection a single small specimen (Pl. 25. fig. 2) of this common Australian species.

*Register No. and Locality*. VIII. 4, Sandy Isle.

## Genus ASCOLEUCETTA n. gen.

Leucascidæ with a well-developed dermal cortex densely packed with large and small triradiates and pierced by well-defined inhalant apertures guarded each by a fringe of hair-like oxea projecting radially inwards from within the margin. The elongated and much branched flagellate chambers are more or less radially arranged around the wide exhalant canals, which open by numerous oscula.

## 3. ASCOLEUCETTA COMPRESSA n. sp. (Pl. 25. fig. 3; Pl. 26. figs. 2, 3, 4, 5.)

The sponge, which measures 25 mm. in height, 22 mm. in greatest width, and has an average thickness of 4 mm., forms an erect, compressed, irregular, more or less lobulated mass. The surface is smooth but uneven, and sieve-like in appearance owing to the presence of numerous small, circular, inhalant apertures, about 0.2 mm. in diameter, which are closely and uniformly scattered all over it. The oscula, which measure about 1 mm. in diameter, are arranged singly and are for the most part marginal. Colour in spirit light greyish brown; texture firm and compact, rather hard.

The inhalant apertures (Pl. 26. fig. 5) pierce the well-developed dermal cortex, which is about 0.13 mm. in thickness, and lead into large, well-defined inhalant canals which run in between the flagellate chambers. The latter are much elongated and copiously branched; they tend to be radially arranged round the larger exhalant canals, with their blind ends directed more or less at right angles towards the dermal surface (Pl. 26. figs. 3, 4). The chambers, whose walls are pierced by numerous prosopyles, open into wide exhalant canals which lead up to the vents. The collared cells are basinucleate and confined to the radial chambers, being absent from the exhalant canals.

The skeleton consists of triradiates and quadriradiates, for the most part equiangular and equiradiate. The dermal cortex (Pl. 26. fig. 5) contains numerous large triradiates arranged tangentially, intermingled with small triradiates which are packed in a dense feltwork around the margins of the inhalant apertures. These apertures are guarded by a fringe of hair-like oxea projecting radially inwards from the margin in small groups (Pl. 26. fig. 5). There are no large spicules in the interior of the sponge, small tri- and quadriradiates being scattered closely but irregularly in the walls of the radial chambers and exhalant canals, the facial rays lying tangentially, while the slender apical rays of the quadriradiates project into the chambers and into the exhalant canals.

*Spicules*:—(1) Large triradiates (Pl. 26. fig. 2a); with conical, straight or slightly crooked, gradually or sometimes rather abruptly sharp-pointed rays, measuring about 0.35 by 0.052 mm.

(2) Small triradiates (Pl. 26. fig. 2b); with straight, conical, bluntly pointed rays, measuring up to 0.14 by 0.03 mm. All the triradiates are



equiangular and more or less equiradiate, but sometimes the rays become slightly unequal.

(3) Quadri-radiates of three kinds: (a) (Pl. 26. fig. 2 c), regular, very abundant, like the small tri-radiates with the addition of a slender, curved, often crooked, apical ray; the facial rays measure about 0.15 by 0.035 mm.: (b) (Pl. 26. fig. 2 d), sagittal, with a wide oral angle and a slender, backwardly directed, very slightly curved apical ray; the oral rays (which measure up to 0.13 by 0.02 mm.) are sometimes slightly curved, the basal ray is slightly shorter than the oral and straight and conical; these spicules are not very abundant and are probably confined to the exhalant canals and the oscular margin: (c) (Pl. 26. fig. 2 e), sagittal, small, very irregular, usually with curved, crooked rays, measuring about 0.1 by 0.019 mm. (b) and (c) have only been found in boiled-out preparations.

(4) Trichoxea (Pl. 26. fig. 5, tr.) very slender, sharp-pointed, measuring about 0.16 mm. in length.

*Register No. and Locality.* III. 12, Wooded Isle.

#### 4. *LEUCETTA CHAGOSSENSIS* Dendy.

*Leucetta chagosensis* Dendy [1913].

There are two specimens in the collection. One (R.N. II. 4), which measures 32 mm. in length, 16 mm. in height, and has an average thickness of 8 mm., is compressed and irregular, proliferating into short, nodular processes; the vents, which have slightly prominent margins, are scattered and vary in size between 1 and 2 mm. The second specimen (R.N. II. 5 b) consists of three small lobose fragments which have been broken off a larger specimen.

The Abrolhos specimens agree closely with the type except that the ectosome is thinner and the subdermal cavities slightly smaller. Numerous embryos are present, the structure of which indicates clearly that the larva of *Leucetta* is a parenchymula.

*Previously known Distribution.* Chagos Archipelago, Indian Ocean (Dendy).

*Register Nos. and Locality.* II. 4, II. 5 b, Wooded Isle.

#### 5. *LEUCETTA MICRORAPHIS* Haeckel.

*Leucetta primigenia* var. *microraphis* Haeckel [1872].

*Leuconia dura* Poléjaseff [1883].

*Leucetta primigenia* var. *microrrhaphis* Ridley [1884].

*Leucetta microrrhaphis* Lendenfeld [1885].

*Leucandra microrrhaphis* Dendy [1892].

*Leucetta microraphis* Dendy & Row [1913].

The single specimen consists of a small, oblong fragment measuring about 22 by 10 mm.; at one end there is a small slit-like vent measuring about 2 by 1 mm. Colour in spirit light brown; texture very hard and coarse.

The skeleton consists of tri-radiate spicules only; these are of two sizes and scattered irregularly throughout the sponge except at the surface, where

they are arranged tangentially. The rays of the large triradiates measure up to 1.1 by 0.23 mm., those of the smaller 0.18 by 0.013 mm.

*Previously known Distribution.* Bermudas (*Poléjaeff*); Australia (*Poléjaeff*, *Ridley*, *Lendenfeld*, *Dendy*).

*Register No. and Locality.* VI. 17 b, Sandy Isle.

#### 6. *LEUCALITIS OLATHRIA* *Haeckel*.

(For literature and synonymy *vide* *Dendy* and *Row* [1913].)

There are two very fine specimens of characteristic external form, each measuring about 80 mm. in diameter.

*Previously known Distribution.* See *Dendy* [1913].

*Register No. and Locality.* III. 3, IV. 2, Wooded Isle.

#### 7. *SYCON GELATINOSUM* *de Blainville*.

(For literature and synonymy *vide* *Dendy* and *Row* [1913].)

There are six specimens of this common Australian species in the collection, usually forming colonies of several or many persons, but varying considerably in the size of person and in the way in which the colony branches; the largest person measures 25 mm. in height and 12 mm. in greatest diameter.

The colour in spirit varies from light yellowish brown to dull greyish brown. The oscula are all provided with a fringe of spicules.

There is one specimen (R.N. VII. 1 d) consisting of a single person only; it is 16 mm. in height and has an average diameter of 7 mm.; the colour in spirit is almost white.

The internal structure and spiculation of all the specimens are typical.

*Previously known Distribution.* Australia (various authors and collections); Java (*Haeckel*).

*Register Nos. and Localities.* II. 2, II. 5 a, III. 2, III. 13 a, III. 13 b, Wooded Isle; VII. 1 d, Sandy Isle.

#### 8. *VOSMAEROPSIS MACKINNONI* n. sp. (Pl. 25. fig. 4; Pl. 26. fig. 6.)

Sponge (Pl. 25. fig. 4) colonial, consisting of a number of short, thick, subcylindrical individuals united together in an irregular manner along a greater or lesser portion of their length. Each individual has a circular or oval osculum at its summit; in perfect individuals a beautiful oscular fringe is present, formed of very long, hair-like oxea; in others this fringe is broken off short. The individuals vary rather in size owing to their peculiar branching and colonial habit; an average full-grown person is 15 mm. in height and 3 mm. in diameter, the thickness of the wall being 1.3 mm. The outer surface is rough and uneven, and large oxea can be seen projecting irregularly from it; these oxea are more or less absent from the basal portions of the sponge, where the surface is much more even and only slightly roughened. Colour in spirit pale brown; texture rather fragile.

Both dermal and gastral cortices are well developed, the former about 0.18 and the latter about 0.1 mm. thick. Between these lies the chamber layer with a thickness of about 1 mm.

The canal system is "syllleibid," the elongated flagellate chambers, up to 0.4 mm. in length, opening into wide exhalant canals, which interdigitate with the main inhalant canals running in from beneath the dermal cortex. Small, scattered dermal pores lead into much narrower inhalant canals, which pierce the dermal cortex to open into the wide outer ends of these main inhalant canals.

The collared cells are apicinuclate.

The skeleton of the dermal cortex consists of tangentially placed triradiates of various sizes, beneath which lie the short rays of the subdermal pseudosagittal triradiates.

The skeleton of the gastral cortex consists exclusively of rather slender triradiates arranged tangentially, which become strongly sagittal (alate) towards the osculum, with the oral arms extended parallel with the margin of the latter.

The skeleton of the chamber layer consists of (1) the contripetally directed rays of the large subdermal pseudosagittal triradiates, (2) very large and stout subgastral sagittal triradiates, (3) similar triradiates whose paired rays lie at a variable distance beneath the gastral cortex, (4) the inner portions of the large oxea, whose outer portions project through the dermal cortex.

*Spicules*:—(1) Triradiates of the dermal cortex (Pl. 26. fig. 6 *d*); approximately regular, with conical, gradually tapering, sharply-pointed rays, measuring from about 0.23 by 0.026 to 0.4 by 0.04 mm.

(2) Triradiates of the gastral cortex (Pl. 26. fig. 6 *e*); approximately regular and more or less strongly sagittal; much smaller on the average than those of the dermal cortex, with slender, gradually tapering, sharply-pointed rays measuring about 0.21 by 0.013 mm.

(3) Subdermal pseudosagittal triradiates (Pl. 26. fig. 6 *e*); the three rays are all different; the true basal ray, now forming a false pair with one of the orals, is the shortest of the three and straight or nearly so, conical and gradually sharp-pointed, measuring, say, 0.21 by 0.026 mm.; the oral ray which forms an apparent pair with the basal is rather longer, measuring, say, 0.26 by 0.026 mm., and more or less crooked; the other oral ray, now centripetally directed, is much longer and more slender, measuring, say, 0.5 by 0.02 mm., perfectly straight and gradually sharp-pointed.

(4) Subgastral sagittal triradiates (Pl. 26. fig. 6 *b*); very large and stout, rays conical, gradually and sharply pointed, oral rays often slightly curved or crooked, basal ray (centrifugally directed) longer than orals; oral rays measuring, say, 0.41 by 0.04 mm., with basal 0.52 by 0.05 mm., but variable.

(5) More distal triradiates of the chamber layer (Pl. 26. fig. 6 *b*); not sharply distinguishable from (4), but usually with shorter basal rays and straighter orals.

(6) Large oxea (Pl. 26, fig. 6a), echinating the outer surface of the sponge; stout, curved, often crooked, especially the outer part, the inner portion being straighter and tapering more gradually; fairly sharply pointed at each end; measuring up to 1.2 by 0.06 mm.

(7) Oxea of the peristomial fringe; very long and slender, hair-like, usually broken off; measuring up to 2.3 by 0.009 mm.; outer ends hastate, very sharply pointed.

It is quite possible that this species may prove to be identical with one or other of two species in the Hamburg South-west Australian collection for which the late Mr. Row proposed the names *Vosmaeropsis dendyi* and *V. primitiva*. These names are given in Dendy and Row's "Classification and Phylogeny of the Calcareous Sponges" [1913], but no descriptions have yet been published. Beyond the fact that the species in question belong to the same section of the genus as *V. mackinnoni*, it is impossible at the present time to say anything about them, as the specimens have been sent to Japan for further investigation by Dr. Sanji Hōzawa.

*Register No. and Locality.* IV. 1, Wooded Isle.

9. *GRANTIOPSIS CYLINDRICA* Dendy. (Pl. 25. figs. 5, 6, 7, 8; Pl. 26. fig. 7.)

*Hypograntia infrequens* Carter [1885-6].

*Grantiopsis cylindrica* Dendy [1892, 1893 A].

*Grantiopsis cylindrica* Dendy & Row [1913].

*Grantiopsis infrequens* Dendy & Row [1913].

There are five specimens in the collection, which vary slightly in size and appearance; each consists of a single person only.

R.N. I. 1 (Pl. 25. fig. 8) is typical; it is attached to a rock by its base, and forms a slightly curved, cylindrical tube, 20 mm. long and 5 mm. in diameter, with a slightly constricted, terminal osculum, almost without fringe; the wall of the tube is 1 mm. in thickness. The surface is almost smooth, with a characteristic glistening appearance due to the presence of the large tangential triradiates. Colour in spirit almost white; texture firm and compact, but brittle. Other typical specimens are shown in figs. 5-7.

The skeleton arrangement, the form and size of the spicules, and the canal system agree closely with those of the type of the species as described by Dendy [1892], and a detailed description is therefore not necessary. As, however, the spicules have not as yet been figured separately, but only in the transverse section given by Dendy [1893 A], we take this opportunity of supplementing his description with the necessary illustrations (Pl. 26. fig. 7, a-h; *vide* also Description of Plates).

In their "Classification and Phylogeny of the Calcareous Sponges" [1913], Dendy and Row have pointed out that Carter's *Hypograntia infrequens* is undoubtedly a species of *Grantiopsis*, but, according to Mr. Row's observations on material collected by the Hamburg South-west Australian Expedition,

different specifically from *G. cylindrica*. We are now in a position, however, as the result of microscopical examination of the very small, fragmentary type in the British Museum, to state that *Hypograntia infrequens* and *Grantiopsis cylindrica* are specifically identical. This being the case, it might be argued that both the generic and the specific names proposed by Carter should take priority.

As to the generic name *Hypograntia*, it must be pointed out, in the first place, that the diagnosis of this genus contains nothing that is distinctive, and is founded upon an obvious error with regard to the structure of the canal-system, and, in the second place, that although *Hypograntia infrequens* is the first of six species described in the same paper, it is said to be "*incertæ sedis*," so that it cannot reasonably be regarded as the type of the genus, and as it is quite distinct generically from the five remaining species, it seems advisable to retain the generic name *Grantiopsis* (originally regarded as a subgenus of *Grantia*).

As to the specific name *infrequens*, it must be pointed out that Carter's description of the species is quite unrecognisable. He altogether omits the most characteristic feature of the sponge, viz. the reduced tubar triradiates, and describes the subgastral quadriradiates as triradiates. It was only the fact that we happened to have access to Mr. Carter's manuscript drawings that put us on the track of the identification. Even in these drawings the reduced tubar triradiates are not shown. Had the identification been established before the publication of the name *Grantiopsis cylindrica*, it would doubtless have been better to call the species *Grantiopsis infrequens*, but as the former name has now become established in the literature and as Mr. Carter's species was not recognisably described, we see no sufficient reason for reverting to his name.

*Previously known Distribution.* Port Phillip Heads (*Dendy, Carter*).

*Register No. and Locality.* I. 1, VI. 17 c, VII. 1 a, VII. 1 b, VII. 1 c, Sandy Isle.

9 a. *GRANTIOPSIS CYLINDRICA* Dendy var. *FRUTICOSA* nov. (Pl. 25. fig. 9.)

The specimen, which is colonial, branched and bushy, consists of about 14 persons united together at their bases by short connections; each person forms a slightly curved cylindrical tube with a circular osculum at the summit without projecting fringe; the persons average only 12 mm. in length, with a nearly uniform diameter of 3.5 mm.; they have an almost smooth surface, with a characteristic glistening appearance due to the presence of the large tangential triradiates. Colour in spirit very pale coffee-brown; texture compact and firm. The skeleton arrangement, canal system and spiculation agree so closely with those of the typical form that no detailed description is necessary.

The variety differs from the type of the species chiefly in its bushy habit and the smaller size of the individual persons, but also in that the dermal

cortex forms only about one-third of the total thickness of the tube as compared with about half in the typical form, while the spicules generally are slightly smaller and the rays of the large dermal triradiates somewhat shorter and blunter.

*Register No. and Locality.* III. 4, Wooded Isle.

10. *LELAPIA ANTIQUA* n. sp. (Pl. 25. fig. 10 ; Pl. 26. fig. 8.)

The single specimen, which is attached by its lower end to a piece of calcareous debris, measures 20 mm. in height and 10 mm. in greatest diameter. It is erect, club-shaped, somewhat curved upon itself and slightly flattened in one plane. The single oval osculum, which measures 3 by 2 mm., is nearly terminal in position and has a well-developed, collar-like peristome. The surface of the lower two-thirds of the sponges is smooth ; that of the upper third is coarsely and unevenly hispid, owing to large projecting brushes of long, slender oxea. Colour in spirit light yellowish grey ; texture firm.

The dermal cortex is about 0.42 mm. thick, the gastral cortex about 0.13 mm., and the chamber layer, between the two, about 1.95 mm.

There appear to be numerous small dermal pores scattered over the surface, but now very difficult to recognize. Short and narrow canals lead from the surface into large and very irregular crypts in and beneath the dermal cortex, from which the rather wide inhalant canals run radially inwards. The canal system is typically leuconoid. The flagellate chambers, thickly scattered in the clear, gelatinous mesogloea, are oval and about 0.1 mm. in longer diameter. The main exhalant canals open radially into the large central gastral cavity.

The collared cells are apicinuclateo.

The skeleton of the dermal cortex consists of two very distinct parts : (1) several layers of slender-rayed, normal sagittal triradiates, arranged tangentially, the whole about 0.085 mm. thick ; (2) a deeper and thicker part, consisting of longitudinal bundles of huge oxea, the whole about 0.34 mm. thick. The dense brushes of slender oxea that project from the surface may also be included with the skeleton of the dermal cortex.

The skeleton of the chamber layer consists of (1) a confused interlacement of huge oxea, lying in all directions ; (2) radially or subradially arranged fibres or bundles of tuning-fork spicules, with the unpaired rays directed outwards ; (3) the basal rays of subgastral sagittal triradiates.

The skeleton of the gastral cortex consists of several layers of alate triradiates lying tangentially but otherwise without definite arrangement, backed by the oral rays of the subgastral sagittal triradiates.

The skeleton of the peristome is rather remarkable ; there is no fringe of freely projecting spicules, but a thin peristomial membrane supported by a dense but approximately single layer of huge oxea, which are really a continuation of the deeper skeleton of the dermal cortex, lined by a layer of

alate quadriradiates with short apical rays, forming a continuation of the gastral skeleton, but with the paired rays arranged more regularly, parallel with the oscular margin.

*Spicules* :—(1) Normal sagittal triradiates of the dermal cortex (Pl. 26. fig. 8 c) ; with slender, gradually sharp-pointed rays ; the oral angle is very wide and the oral rays measure about 0.23 by 0.014 mm. ; the straight basal ray is longer than the orals and measures, say, 0.4 by 0.013 mm.

(2) Subgastral sagittal triradiates (Pl. 26. fig. 8 c') ; these are like the normal sagittal triradiates except that the rays are stouter and the orals more distinctly recurved ; the orals measure up to 0.3 by 0.026 mm., with the basal 0.5 by 0.03 mm.

(3) Laterally extended (alate) triradiates of the gastral cortex (Pl. 26. fig. 8 d) ; the oral rays are straight or very slightly recurved, gradually sharp-pointed, measuring up to 0.31 by 0.016 mm., and the oral angle is so wide that the rays are almost in the same straight line ; the basal ray is very short, straight and conical, measuring about 0.04 by 0.01 mm.

(4) Alate quadriradiates of the peristome (Pl. 26. fig. 8 e) ; these are similar to the alate triradiates, with the addition of a very short, straight, sharp-pointed apical ray.

(5) "Tuning-fork" spicules (Pl. 26. fig. 8 f) ; with straight, slender, gradually sharp-pointed rays ; the basal ray is the longest and stoutest, measuring about 0.4 by 0.009 mm. ; the two oral rays, which are slightly unequal in length, run straight forward parallel to one another ; the longer of the two measures about 0.21 by 0.006 mm.

(6) Large stout oxea (Pl. 26. fig. 8 a) ; fusiform, slightly curved, sometimes a little irregular in shape and diameter, tapering gradually to a sharp point at each end ; full-grown spicules measure up to 2.0 by 0.09 mm.

(7) Slender oxea of the dermal brushes (Pl. 26. fig. 8 b) ; straight or very slightly curved, gradually sharp-pointed, sometimes slightly hastate, measuring up to 1.6 by 0.007 mm., but often less.

This species closely resembles *Lelapia australis* Carter, as described and figured by Dendy [1893 B], but differs in the absence of microxea ("mortar spicules") and in the presence of a definite layer of large, longitudinally placed oxea in the deeper part of the dermal cortex. In the latter respect it occupies an intermediate position between *Lelapia australis* and *Lelapia nipponica*, a remarkable Japanese species described by Hara [1894]. We have been unable to obtain access to the description of this species, but, thanks to the kindness of Dr. Hôzawa, have been able to examine a number of transverse sections\*. It is obvious that *Lelapia nipponica* is a much more primitive species than *L. australis*. The bundles of "tuning-fork" spicules are arranged almost strictly radially, with the unpaired rays centrifugally directed, and clearly represent the articular tubar skeleton, though the canal

\* Since this paper was read, Dr. Hôzawa [1923] has published an illustrated description of the Japanese species and proposed for it the new genus *Paralapia*.

system is already of the leuconoid type. The large oxea are confined to the dermal cortex, where they form a well-defined layer, and have not yet invaded the chamber layer as in *L. australis* and, to a less extent, in *L. antiqua*. There are other minor differences distinguishing *L. nipponica* from either of the Australian species, but the material in our possession is not sufficient to elucidate all these.

It is clear that *Lelapia antiqua* is intermediate in structure between the more primitive *L. nipponica* and the less primitive *L. australis*, and it is interesting to note that it also occupies an intermediate position geographically, *L. australis* having been found so far only off the Victorian coast.

*Register No. and Locality.* VII. 1e, Sandy Isle.

#### 11. *DERCITOPSIS MINOR* Dendy [1916 B].

There is one specimen in the collection. The sponge, which measures 42 mm. in length, 25 mm. in breadth, and has an average thickness of 7 mm., forms an irregular, oval, cushion-like mass, concave below, and probably grew on the back of a crab. The margins are broadly rounded. The surface is smooth and minutely punctate. The vents are small and few in number, scattered singly over the upper surface. Inhalant pores are closely scattered over the surface. Colour of surface in spirit varying from light brown to dark slate-grey, internally dull yellow; texture firm and compact.

The skeleton consists of a dense feltwork of loose spicules irregularly arranged except at the surface, where there is a dermal layer of perpendicularly arranged oxea. The spiculation agrees closely with that of the type.

The ectosome and choanosome are not sharply differentiated, but the former contains many more spicules. There is no fibrous tissue in the ectosome. The mesogloea of the choanosome is finely and uniformly granular. The dermal pores lead into short inhalant canals, which penetrate the ectosome and lead into large crypts from which the inhalant canals of the choanosome originate. The canal system is diplodal, not eurypylous as described for *Dercitopsis ceylonica* Dendy. The flagellate chambers are large and pouch-like, with a short wide aphodus and a short narrow prosodus; they measure about 0.04 mm. in longer diameter. The exhalant and inhalant canaliculi of the chambers are lined by flattened epithelium, the nuclei of which can be seen. The collared cells are apicinnucleate. Small round testes are scattered in the deeper parts of the choanosome, in which spermatogenesis is clearly shown. Tailed spermatozoa are present. There is no trace of ova, so the species is probably dioecious.

*Previously known Distribution.* Indian Ocean (*Dendy*).

*Register No. and Locality.* II. 1, Wooded Isle.

#### 12. *DERCITOPSIS MAMMILLARIS* (Lendenfeld).

*Plakinastrella mammillaris* Lendenfeld [1906].

*Dercitopsis mammillaris* Dendy [1916 B].

The single specimen is of depressed cushion-like form, and has apparently been attached by a broad base to the vertical side of a rock, for two large



oval vents, 3.5 mm. in diameter, with slightly prominent margins, occur on one edge. Microscopic inhalant pores are thickly scattered over the smooth surface. Colour in spirit light greyish brown; texture firm and compact.

The skeleton consists of a thick feltwork of loose, irregularly arranged spicules. There is a dense layer of oxea at the surface, largely but not entirely radially arranged.

*Spicules*:—(1) Tetracts; with smooth, sharp-pointed rays measuring from 0.093 to 0.2 mm. in length and from 0.018 to 0.04 mm. in thickness.

(2) Diaets (oxea): smooth, fusiform, slender, slightly curved, gradually sharp-pointed, sometimes with a kink or an enlargement near the middle, measuring from 0.06 to 0.14 mm. in length and from 0.004 to 0.005 mm. in thickness. The oxea are more numerous than the tetracts. Triacts are absent.

The dermal pores lead into short, narrow, inhalant canals piercing the densely spiculated ectosome, beneath which they unite to form sub-cortical crypts from which the inhalant canals of the choanosome originate. The canal system is diplodal, the aphodi and prosodi being longer and narrower than in *Derritopsis minor* Dendy. The flagellate chambers are sub-spherical, measuring about 0.04 mm. in diameter. The narrow exhalant canals gradually pass into wider ones, which in turn open into the wide oscular tubes. The main inhalant canals are surrounded by collenchymatous mesogloea devoid of spicules; the main exhalant canals are probably like the inhalant, but as no sections have been taken through a vent this cannot be proved. The mesogloea between the chambers is finely granular.

Testes are irregularly scattered in the choanosome; they are rounded sacs lined by an epithelium and containing various stages in the development of spermatozoa. Segmenting embryos are also present; the sponge is therefore hermaphrodite and presumably protogynous.

*Previously known Distribution.* West coast of Australia (*Lendenfeld*).

*Register No. and Locality.* II. 13, Wooded Isle.

### 13. *STELLETTA BREVIS* Hentschel [1909].

The single specimen, a cushion-like mass which has probably been torn off a rock, measures 38 mm. in length, 25 mm. in breadth, and 15 mm. in thickness. Surface smooth but finely granular. Oscula not visible. The surface colouring in spirit varies from a very light brown to a violet-grey, that of the interior is light brown.

The sponge possesses a well-developed cortex. Immediately beneath the surface is a thin layer of strongylasters, then comes a non-fibrous portion filled with minute brown pigment granules and containing inhalant chones; below this is a light-coloured, non-pigmented, fibrous layer. Between the cortex and the choanosome are large sub-cortical crypts. The choanosome, in which oxyasters are thickly scattered, contains narrow inhalant canals.

The skeleton, which agrees closely with that of Hentschel's South-West Australian specimen, consists of radially arranged bundles of plagiotriænes and oxea; in the deeper parts there is less regularity. The spicules resemble closely those of the type in size and appearance.

*Previously known Distribution.* Sharks Bay, S.W. Australia (*Hentschel*).

*Register No. and Locality.* VI. 8, Sandy Isle.

14. *STELLETTA DEBILIS* Thiele.

*Stelletta debilis* Thiele [1900].

*Stelletta debilis* Lendenfeld [1903].

The single complete specimen is sub-spherical in shape, measuring 15 mm. in diameter. There is a single oval osculum, 2 mm. long and 1 mm. broad, near the point of attachment of the sponge to a piece of rock. Inhalant pores are thickly scattered all over the slightly roughened surface between the cladi of the triænes. Colour in spirit light brown; texture firm and compact, but compressible.

There is a slightly fibrous cortex, and the skeleton is radially arranged and quite typical.

*Spicules* :—(1) Orthotriænes; shaft straight or nearly straight, tapering gradually to a sharp point, measuring 1.35 by 0.026 mm.; cladi sharply pointed, recurving at once so as to extend at right angles to the shaft, measuring 0.16 mm. in length.

(2) Anatriænes; these frequently project beyond the surface of the sponge; shaft long, slender, slightly curved, measuring 1.3 by 0.015 mm.; cladi well developed and markedly recurved, measuring 0.052 mm. in length.

(3) Oxea; fusiform, usually curved, sharp-pointed, measuring 1.1 by 0.02 mm.; these are most abundant in the deeper parts of the sponge.

(4) Oxyasters; with 6 to 10 slender, sharp-pointed rays and no distinct centrum; diameter 0.017 mm.; these are scattered sparsely throughout choanosome and ectosome.

*Previously known Distribution.* Ternate (*Thiele*).

*Register No. and Locality.* II. 16, Wooded Isle.

15. *STELLETTA SIGMATRIÆNA* Lendenfeld [1906].

There are two small, complete specimens, sub-spherical in shape, 12 and 8 mm. in diameter respectively. Inhalant pores, visible with a lens, are scattered evenly over the smooth surface. Each specimen has one minute oval osculum lying in a slight depression. Colour in spirit buff.

The skeleton consists of radially arranged oxea and triænes, not concentrated into bundles. Just beneath the surface the cladi of the triænes form a sharply-defined layer; their shafts pierce the region of the chones, which is cladome-free. In the choanosome are radially placed anatriænes, orthotriænes in various stages of development, and less regularly arranged oxea.

*Spicules* :—(1) *Orthotriaenes* ; shaft straight, gradually pointed, measuring about 1·1 by 0·015 mm. ; the cladi, which are about 0·3 mm. long, at first form with the shaft an angle of about 120°, but somewhere along their length they abruptly turn back so that their distal ends are at right angles to the shaft.

(2) *Anatriaenes* ; shaft straight, gradually tapering to a sharp point, measuring about 1·1 by 0·03 mm. ; the sharply-pointed cladi, which are about 0·15 mm. long, curve outwards almost at right angles to the shaft and then run back parallel to it.

Our specimen contains only a few of the irregular *orthotriaenes* and of the sigma-like *anatriaenes* figured by Lendenfeld in his 'Valdivia' report.

(3) *Oxea* ; straight or slightly curved, bluntly pointed, measuring about 1·1 by 0·015 mm.

(4) *Oxyasters* ; of two kinds—(a) large, with 2 to 6 fairly stout, roughened, bluntly pointed rays, total diameter about 0·02 mm. ; these are most abundant just beneath the inhalant chones : (b) small, with 6 to 10 thin, very minutely roughened rays ; total diameter 0·014 mm. These are scattered through the choanosome, but not abundantly.

*Previously known Distribution.* Dirk Hartog, W. Australia (*Lendenfeld*).

*Register Nos. and Localities.* IV. 8, Wooded Isle ; VI. 18c, Sandy Isle.

#### 16. *ANCORINA AUSTRALIENSIS* (Carter). (Pl. 25. fig. 11.)

*Stelletta australiensis* Carter [1883].

*Ecionema australiense* Sollas [1885].

*Ancorina australiensis* Lendenfeld [1903].

There are four specimens in the collection. The largest (R.N. VI. 6a ; Pl. 25. fig. 11) forms an incomplete cone, 40 mm. in height, with a base measuring 60 by 70 mm. ; the apex is truncated, and over the flattened area thus formed, which measures 40 by 25 mm., are scattered numerous open vents which vary in diameter from 0·25 to 1 mm. Part of the side of the cone is encrusted by *Spongelia dakini* n. sp. The second specimen (R.N. I. 3) is irregularly massive and measures 80 by 60 by 50 mm. ; its upper surface is almost entirely covered by an encrusting *Reniera* and a mass of other débris. The third specimen (R.N. II. 6) measures 40 by 45 by 25 mm., and is largely overgrown by a mass of other organisms. The fourth (R.N. III. 6) an irregular, cake-shaped mass, measures 85 by 50 by 40 mm. ; its upper surface is uneven and slightly wrinkled.

No vents are visible except in the figured specimen ; inhalant pores, visible with a pocket lens, are scattered in groups of two or three over the smooth upper surface of all the specimens ; they are most marked in the figured specimen. Colour in spirit purplish brown on outside, light yellowish brown inside ; texture firm and compact.

The skeleton consists of radially arranged *triaenes* and *oxea*, with a layer of small ectosomal *oxea* vertical to the surface. The microrhabds are

thickly scattered through the ectosome and choanosome, as well as forming a well-developed dermal layer. Large brown pigment granules are scattered throughout all four specimens.

The form and size of the spicules agree closely with Sollas's description of Carter's specimen.

*Previously known Distribution.* Fremantle, West Australia (Carter).

*Register Nos. and Localities.* VI. 6 a, Sandy Isle; I. 3, Turtle Bay; II. 6, III. 6, Wooded Isle.

17. *ANCORINA BREVIDENS* n. sp. (Pl. 26. fig. 9.)

The single specimen, which is about 60 mm. long, 40 mm. wide, and 20 mm. thick, is massive and potato-shaped; at one end is a group of about twenty small, close-set oscula, which average about 1 mm. in diameter. The surface is smooth, a large portion of it being covered with foreign matter of varying kind. Colour in spirit purplish grey; texture hard, compact, slightly compressible.

The ectosome forms a cortex about 0.5 mm. thick, with numerous cortical crypts in its deeper portion; the cortex appears to be only slightly fibrous, but contains numerous brown granular pigment cells, which occur also in the outer portion of the choanosome.

The main skeleton consists of close-packed, radial bundles of oxea and triænes: the cladi of the triænes occur at various levels in and just below the cortex, but chiefly just beneath the surface. The outer part of the cortex contains numerous comparatively small, slender, radially arranged oxea. There is a dense dermal layer of microrhabds, and both microrhabds and tylasters are abundantly scattered through ectosome and choanosome.

*Spicules*:—(1) Orthotriænes (Pl. 26. fig. 9 a); shaft long, straight or slightly curved, tapering gradually to a fine point (sometimes blunted), measuring about 2.2 by 0.05 mm.; cladi gradually but bluntly pointed, measuring about 0.16 by 0.04 mm.

(2) Anatriænes (Pl. 26. fig. 9 b); shaft very long, slender, tapering very gradually to a finely pointed or blunted extremity, measuring about 3.0 by 0.02 mm.; cladi very much reduced in length, bluntly pointed, measuring about 0.026 by 0.017 mm.

(3) Oxea of two sizes; the larger (Pl. 26. fig. 9 c) fusiform, curved, gradually and sharply pointed, measuring about 2.3 by 0.04 mm.; the smaller (Pl. 26. fig. 9 c') found only in the cortex, straight, sharp-pointed, measuring about 0.34 by 0.009 mm.

(4) Microrhabds (Pl. 26. fig. 9 d); roughened, slightly swollen in centre, measuring about 0.011 by 0.003 mm..

(5) Tylasters (Pl. 26. fig. 9 e); some have 6 to 8 slender rays with very small heads and no centrum; others, which are slightly smaller, have more rays and a small centrum; the average diameter of the entire spicule is 0.013 mm.

This species is evidently very closely related to *Stelletta truncata* Kieschnick [1898] = *Ancorina amboinensis* Lendenfeld [1903], from Amboina, in the Malay Archipelago, differing in the great abbreviation of the cladi of the triænes, especially of the anatriænes.

*Register No. and Locality.* VI. 16 b, Long Island.

#### 18. AURORA ROWI Dendy [1916 B].

There are three lobose pieces which have probably been attached to rock ; the largest measures 40 mm. in length, 20 mm. in breadth and 15 mm. in thickness ; it has a bit of branching coral growing through it. The surface is sub-glabrous and crumpled, with irregular grooves of varying depth running across it. The oscula, which are few in number and single, lie at the apices of small rounded prominences ; they vary in size, the largest being 2 mm. in diameter. Inhalant pores are scattered singly over the surface. Colour in spirit chocolate-brown ; texture compressible but fairly compact.

The skeleton arrangement and spiculation agree with those of the type specimen, the only difference being the occasional occurrence of irregular branching of the cladi of the orthotriænes ; this is not sufficient, however, to justify a specific distinction.

*Previously known Distribution.* Seychelles (Dendy).

*Register No. and Locality.* II. 8, Wooded Isle.

#### 19. ASTEROPUS SIMPLEX [Carter].

(For literature and synonymy *vide* Dendy [1916 B].)

The single specimen is an, irregular, cake-shaped mass, about 80 mm. in maximum diameter. The upper surface is uneven, somewhat ridged and depressed at intervals ; a number of open vents, 1 mm. in diameter, are scattered over it. Colour in spirit purplish brown ; texture firm, compact, coarse.

The skeleton arrangement and spiculation agree with those of the 'Sealark' specimen, and need not be described.

*Previously known Distribution.* Fremantle and Port Phillip Heads, Australia ; Hayti (Carter) ; S.W. Australia (Hentschel) ; Indian Ocean (Dendy).

*Register No. and Locality.* VI. 5, Sandy Isle.

#### 20. ERYLUS PROXIMUS Dendy [1916 B].

The single specimen, an irregular lobate mass, is 28 mm. in length, 22 mm. in breadth and 15 mm. in thickness. The surface is uneven and punctate, in parts covered with calcareous débris. Scattered singly over an irregular area, near the end where the sponge was probably attached, are many minute, widely open, dermal pores, while over the major portion of the rest of the sponge are numerous white specks, giving the surface its punctate appearance ; these are probably closed inhalant pores. On a prominent part of the upper

surface is a single, round, open vent, 1.5 mm. in diameter. Colour in spirit light greyish brown; texture hard and compact.

The arrangement, form and size of the spicules are similar to those of the type specimen.

*Previously known Distribution.* Cargados, Indian Ocean (*Dendy*).

*Register No. and Locality.* VI. 12 a, Sandy Isle.

## 21. DONATIA ROBUSTA (*Bowerbank*).

*Tetkea robusta* Bowerbank [1873].

*Tethya globostellata* Lendenfeld [1897].

*Tethya cliftoni* Ridley [1884].

*Tethya ingalli* Kirkpatrick [1900].

*Donatia arabica* Topsent [1906].

*Donatia japonica* var. *albanensis* Hentschel [1909].

*Tethya lyncurium* Row [1911].

*Donatia ingalli* Dendy [1916 B].

*Donatia globostellata* Topsent [1918].

(See M. Burton [1923] MS.)

There are three specimens in the collection, greyish white in colour, ranging from 20 to 26 mm. in diameter. The surface of each is only slightly tessellated.

The skeleton consists of radially arranged bundles of typical strongyloxea which spread out beneath the surface in brushes; loose, radially arranged megascleres lie between the bundles.

*Spicules* :—(1) Strongyloxea; measuring about 1.62 by 0.028 mm.

(2) Spherasters; these form a dense cortical layer; they have a large centrum and short conical rays; diameter about 0.1 mm.

(3) Small asters; with short rays which may either bear a crown of short spines or be beset with numerous small spines; the total diameter is from 0.012 to 0.016 mm. These are found in the cortex and the choanosome.

(4) Small asters; with long rays which may either end in a sharp point or be spined terminally. These are confined to the choanosome; but there are many intermediate forms scattered through the sponge.

This species is undoubtedly very closely related to *Donatia lyncurium* (Linnæus), from which it differs in the large size of the spherasters and the greater differentiation of the small asters.

*Previously known Distribution.* Red Sea (*Row*, *Topsent*); Indian Ocean (*Dendy*, *Lendenfeld*, *Ridley*, *Kirkpatrick*); Australia (*Hentschel*).

*Register Nos. and Localities.* II. 11, Wooded Isle; VI. 7, VI. 19, Sandy Isle.

## 22. DONATIA MULTISTELLA (*Lendenfeld*).

*Tethya multistella* Lendenfeld [1888].

*Tethya multistella* Hallman [1914].

This species is represented by one small, sub-spherical specimen, greyish white in colour, 12 mm. in diameter; and a fragment of another, pale brown

in colour and apparently about 30 mm. in diameter. The surface of the former is only slightly tessellated, while that of the latter, as far as can be judged, is fairly smooth but uneven. The cortex of both is lacunar and not densely charged with spicules.

The skeleton consists of radially arranged bundles of stronglyloxea, which penetrate the cortex and spread out in brushes beneath the surface; loose radially arranged megasccleres are scattered between the bundles.

*Spicules* :—(1) Strongyloxea of the usual type, measuring about 1.26 by 0.016 mm.

(2) Spherasters; about 0.06 mm. in diameter, with conical, sharp-pointed rays, nearly as long as the diameter of the centrum.

(3) Small asters of cortex and choanosome; these range from tylasters, with the ends of the rays beset with small spines, to oxyasters. The diameter of the small aster varies from 0.01 to 0.012 mm.

This species is undoubtedly closely related to *Donatia robusta* (Bowerbank), but differs from it in the size of the spherasters and in small differences in the small asters.

*Previously known Distribution.* Port Jackson, N.S.W. (*Lendenfeld, Hallmann*); Port Phillip Heads (*Hentschel*).

*Register Nos. and Locality.* VI 17 a, VII. 1 f, Sandy Isle.

### 23. *CHONDRILLA AUSTRALIENSIS* Carter.

(For literature and synonymy *vide* Dendy [1916 B].)

There are two small specimens in the collection; one is buff-coloured in spirit, the other liver-brown. The external form and spiculation agree closely with those of the type.

*Previously known Distribution.* Port Jackson, E. Coast of Australia (*Carter, Lendenfeld*); Sharks Bay, S.W. Australia (*Hentschel*); coast of Cochin China (*Lindgren*); Okhamandal, Ceylon, Indian Ocean (*Dendy*).

*Register Nos. and Localities.* VII. 4 a, Turtle Bay; VIII. 1, Sandy Isle.

### 24. *REMERA AQUADUCTUS* (). *Schmidt*. (Pl. 25. fig. 12.)

*Remera aqueductus* Schmidt [1862].

*Remera aqueductus* Kolliker [1864].

*Remera aqueductus* Czerniavsky [1878].

*Remera aqueductus* Swarczewsky [1905].

*Remera aqueductus* Ostroumov [1898].

*Remera aqueductus* Babić [1921, 1922].

The single specimen (Pl. 25. fig. 12), which measures 55 mm. in height, is erect, tubular and thin-walled; at the upper end it divides into two short tubes, each of which terminates in a large round osculum 3 mm. in diameter. Inhalant apertures, visible with a pocket lens, are scattered over the smooth surface. (Colour in spirit greyish brown; texture delicate, spongy, fragile.

The skeleton consists of a somewhat rectangular, unispicular reticulation; towards the outer surface the spicules become concentrated into plurispicular fibres running vertically to the surface.

*Spicules*:—Oxea; small, smooth, straight or slightly curved, sharply pointed, measuring about 0.23 by 0.008 mm.

*Previously known Distribution*. Adriatic (*Schmidt, Babić*); Black Sea (*Czerniarsky, Swartschewsky*).

*Register No. and Locality*. VII. 3, Abrolhos Islands.

## 25. RENIERA CRIBRICUTIS *Dendy* [1921 B].

There are two specimens in the collection, one (R.N. VII. 1 *g*), the colour of which is almost white in spirit, agrees very closely in all respects with the type-specimen, except that it is smaller, measuring 25 mm. in length and 10 mm. in diameter, and has only a single vent, 5 mm. in diameter.

The second specimen (R.N. VIII. 2) consists of two fragments, lobate in appearance, each possessing one large, round osculum, about 4 mm. in diameter, with a slightly raised margin, opening out of a wide oscular tube. This specimen, which is light brownish yellow in colour, does not conform so closely to the type, the subdermal cavities being smaller and the primary lines of the skeleton less differentiated. We feel justified, however, in making the identification.

The spicules of the Abrolhos specimens are of much the same size as those of the type, measuring about 0.14 by 0.006 mm.

*Previously known Distribution*. Amirante, Indian Ocean (*Dendy*).

*Register No. and Locality*. VII. 1 *g*, VIII. 2, Sandy Isle.

## 26. RENIERA PERMOLLIS (*Bowerbank*).

*Isodictya permollis* Bowerbank [1866, 1874, 1882].

*Reniera permollis* Topsent [1888].

*Reniera permollis* Dendy [1916 A].

We identify with this species seven specimens of an encrusting nature which vary considerably in size and general appearance. The surface is slightly hispid, and the large subdermal cavities can be seen through the thin dermal membrane, which is almost aspiculous. The oscula are small, single and scattered, measuring up to about 3 mm. in diameter. The colour in spirit varies from light yellowish brown to nut-brown; texture in most cases very soft and friable, that of R.N. VI. 17 *d* and R.N. VI. 17 *e* firm and compact.

The skeleton arrangement and spiculation agree closely with those of specimens from Okhamandal, but the tendency to form primary lines is not so strongly marked.

*Previously known Distribution*. European seas (*Bowerbank, Topsent*); Okhamandal, Indian Ocean (*Dendy*).



*Register Nos., Localities, etc.* VI. 17 *d*, VI. 17 *e*, Sandy Isle; II. 7 *b*, III. 11, IV. 6, IV. 7, IV. 10, Wooded Isle.

**RENIERA spp.**

There are also in the collection a number of more or less fragmentary specimens representing other species of this difficult genus.

*Register Nos., Localities, etc.* I. 3, VII. 4 *b*, Turtle Bay; VI. 14, VI. 15 *b*, Sandy Isle.

**27. PETROSIA DURA (Nardo) Vosmaer [1887].**

*Reniera dura* Nardo.

*Reniera* ? *dura* Nardo, Schmidt [1862].

*Schmidtia dura* Balsamo Crivelli [1868].

*Schmidtia dura* Schmidt [1868].

*Petrosia dura* Topsent [1897].

*Petrosia dura* Ferrar [1914].

*Petrosia dura* Babić [1921, 1922].

The single specimen in the collection consists of a somewhat irregularly shaped, digitiform fragment, 40 mm. long and 10 mm. thick, which had probably been growing erect and has evidently been cut off transversely from a larger sponge. The surface is smooth, and the dermal membrane, which is thin but distinct, is pierced by inhalant pores visible with a lens. There are two round oscula, 2 mm. in diameter. Colour in spirit light reddish brown; texture hard but brittle.

The skeleton arrangement and spiculation agree closely with those of one of Schmidt's specimens in the British Museum.

The spicules are oxea, which show a great tendency to become rounded off at one or both ends; they measure about 0.35 by 0.015 mm.

*Previously known Distribution.* Adriatic (*Schmidt, Babić*); Mediterranean (*Balsamo Crivelli, Topsent*); Cantabrico (*Ferrar*).

*Register No. and Locality.* VI. 16 *a*, Long Island.

**28. HALICHONDRIA PHAKELLIODES n. sp. (Pl. 26. fig. 10.)**

The single specimen consists of a portion of an erect lamella, 190 mm. in height, 75 mm. in width, with a maximum thickness of 8 mm., constricted towards the base of attachment so as to form a very short, thick stalk. The lamella, which has a narrow, very slightly sinuous margin, appears similar on both surfaces, but one has been somewhat cracked and rubbed.

The surface is smooth and practically even, covered everywhere by a very thin, transparent dermal membrane (rubbed off in places), which contains numerous irregularly and loosely scattered tangential oxea. The dermal membrane is dotted with numerous small, round pore-areas, the pores themselves apparently being closed. The oscula are very inconspicuous; they may be represented by minute apertures at the apices of several small

prominences which are sparsely scattered over both surfaces of the sponge. The colour in spirit is light brownish yellow: texture tough, flexible, resilient.

The skeleton consists of loose tracts of spicular fibre running longitudinally and confined to the middle of the lamella; at right angles to these on both sides still looser and less well-defined fibres run outwards towards the surface, where they terminate in loose brushes of spicules, which help to support the dermal membrane.

Numerous loose spicules lie scattered everywhere between the fibres. There is a fair quantity of spongin present, but so pale in colour that it is almost invisible in unstained preparations.

*Spicules*:—*Oxea* (Pl. 26. fig. 10 a); usually slightly curved or angulated and tapering somewhat abruptly at each end to a sharp point; measuring about 0.58 by 0.017 mm. when fully grown, but frequently shorter and especially more slender. These spicules occasionally become stylote, with one end broadly rounded off (Pl. 26. fig. 10 b).

*Halichondria phakellioides* seems to come very near to *Halichondria velamentosa* (Hansen) Lundbeck [1902], a remarkable fact considering that the former is a shallow-water, sub-tropical form, while the latter is found in deep water in the Arctic regions.

*Register No. and Locality.* VI. 1, Sandy Isle.

## 29. *CHALINA PALMATA* (Lamarck).

*Spongia palmata* Lamarck [1813].

*Chalina palmata* Ridley & Dendy [1887].

*Cladochalina euphras* Lendenfeld [1887].

*Chalina palmata* Whitelegge [1901].

? *Ceraochalina retiarumata* Dendy [1905].

There are three small, incomplete specimens in the collection. The sponge is of erect habit, and consists of irregular, digitate processes arising from a narrow base and sometimes branching. The surface is fairly even, slightly hispid, and has a distinctly reticulate appearance. The thin, transparent dermal membrane is pierced by numerous round inhalant pores, which vary considerably in size. The small, round oscula measure up to 2 mm. in diameter, and are for the most part arranged uniserially on the margins. Colour in spirit light brown: texture spongy, tough and fibrous.

The skeleton arrangement agrees closely with that of *Chalina palmata* Ridley and Dendy [1887], except that the dermal reticulation of spicular fibre has a somewhat smaller mesh.

*Spicules*:—*Oxea*; short, slightly curved, gradually sharp-pointed, measuring about 0.07 by 0.004 mm., but often more slender.

After re-examining the type slides of *Ceraochalina retiarumata* Dendy [1905], we think this species may also be identical with *Chalina palmata* (Lamarck).

*Previously known Distribution.* Indian and European Seas (*Lamarck*); Torres Strait (*Challenger*); New South Wales (*Lendenfeld*, *Whitelegge*).

*Register Nos. and Locality.* II. 3, II. 14, II. 17, Wooded Isle.

*CHALINA* sp.

The single specimen, which measures 40 mm. in height and has an average diameter of 10 mm., is erect, shortly digitiform, slightly compressed, with a single round osculum, 3 mm. in diameter, at the apex, to which two long oscular tubes converge. Surface smooth, minutely punctate; inhalant pores close-set, about 0.04 mm. in diameter. Texture firm, compact, resilient. The specimen is almost black on the outside and brown inside, owing to the presence of numerous pigment granules.

The skeleton is very regular; a transverse section shows numerous parallel primary fibres, about 0.06 mm. in diameter, containing a core of well-developed spicules, usually arranged multiseriately and surrounded by a thick coating of spongin. The primary fibres are connected crosswise at very frequent intervals by secondary fibres of less than one spicule's length and usually with only a single spicule in the axis. A few loose spicules are scattered between the fibres. The spicules at the ends of the primary fibres pierce the dermal membrane, which is also supported by a close-meshed network of unispicular fibre.

*Spicules*.—Oxea; fusiform, slightly curved, gradually sharp-pointed, measuring about 0.14 by 0.007 mm.

*Register No. and Locality.* III. 1, Wooded Isle.

*PACHYCHALINA* sp. ?

There is a small, delicate fragment, light brown in colour, which evidently belongs to this genus.

*Register No. and Locality.* II. 10, Wooded Isle.

30. *CERAOCHALINA MULTIFORMIS* *Lendenfeld* var. *MANAARENSIS* *Dendy*.

(For literature and synonymy *vide* Dendy [1905].)

We identify with this variety four pieces which have apparently formed part of an erect, flattened, lamellar specimen, with an irregularly undulating and proliferating surface. The largest piece is 83 mm. high and 55 mm. wide, and the thickness of the lamella is about 6 mm. The surface is glabrous, and the thin dermal membrane is pierced by numerous inhalant pores. The oscula, which measure about 2 mm. in diameter, are fairly numerous and scattered, but confined almost entirely to one surface of the lamella, while some are marginal in arrangement. The colour in spirit is dirty greyish violet; texture firm, rather tough and resilient.

The skeleton arrangement and spiculation agree very closely with those of the type of the variety, so no description is necessary.

*Previously known Distribution (of variety).* Gulf of Manaar and Ceylon (Dendy).

*Register No. and Locality.* I. 2, Turtle Bay.

31. *PHLÆODICTYON ABROLHOSENSIS* n. sp. (Pl. 26. fig. 11.)

The single specimen, which is about 45 mm. long, 35 mm. wide and 12 mm. thick, is somewhat flattened, cake-shaped, and has probably been attached to a rock by its slightly concave under surface. The smooth, convex upper surface gives off numerous very thin-walled fistulæ of varying sizes, the largest being about 15 mm. in length. The diameter of the fistulæ is from 3 to 5 mm.; some of the smaller ones end blindly; these either bear inhalant pores or are young stages of the larger ones, which terminate each in a wide vent. The body generally is covered with a thin rind (dermal membrane), which easily peels off. Colour in spirit greyish brown; texture internally very soft and spongy, distinctly fibro-reticulate.

The skeleton of the interior consists of a loose, irregular, wide-meshed network of multispicular fibre, averaging about 0.065 mm. in diameter. The fibres are compact, the spicules being surrounded by a good quantity of pale-coloured spongin. Numerous loose spicules, mostly arranged in small bundles of one spicule's length, are scattered through the soft ground substance, which also contains many small brown pigment granules. Immediately beneath the surface and parallel with it is an irregular reticulation of similar spicular fibre, which tends to separate from the underlying main skeleton and come away with the dermal membrane when the latter is peeled off. The skeleton of the dermal membrane and that of the walls of the fistulæ consists of a very dense feltwork of single spicules lying tangentially in approximately a single layer.

*Spicules*.—Oxea (Pl. 26. fig. 11); slightly curved, sharply and fairly gradually pointed at each end, sometimes hastate, measuring about 0.22 by 0.006 mm.

This species seems to approach *Phlæodictyon seychellense* Dendy [1921 B] most closely.

*Register No. and Locality.* II. 9, Wooded Isle.

*PHLÆODICTYON* sp.

There are two small fistulæ, light brown in colour, which have evidently been broken off from the surface of a *Phlæodictyon*.

*Register No. and Locality.* VI. 12 c, Sandy Isle.

32. *PSEUDOESPERIA CARTERI* n. sp. (Pl. 26. fig. 12.)

Sponge lobose, elongated (probably horizontally), slightly compressed, with corrugated surface. Vents and pores not seen. The dermal membrane is distinct and thick, overlying the cavernous and coarsely fibrous interior. Colour in spirit brown; texture soft and compressible.

The main skeleton consists of a well-developed, coarse reticulation of stout, compact, multispicular fibre up to about 0.2 mm. in diameter, composed of closely packed megascleres with little or no spongin. The meshes of the reticulation vary much in size, 0.8 mm. being an average diameter. There is a loose dermal reticulation of ill-defined spicular fibre and loose spicules, with more or less dense, radially arranged brushes of slender tylostyles.

*Spicules*:—(1) Tylostyli (Pl. 26. fig. 12 *a*) ; often slightly curved or crooked, with a well-developed oval head separated from the fairly stout shaft by a slight constriction ; fairly gradually sharp-pointed at the apex ; size about 0.28 by 0.008 mm.

(2) Sigmata (Pl. 26. fig. 12 *b*) ; slender, simple and contort, with short, abruptly recurved, sharply-pointed ends. Length about 0.04 mm. from bend to bend.

(3) Large quadridentate anisochelæ (Pl. 26. fig. 12 *c-c''*) ; very numerous, mostly in rosettes, but scattered singly as well. The free end is composed of four short, sharply-pointed teeth which extend more or less at right angles to the shaft, which is markedly curved and fairly stout ; the fixed end is quadrilateral in side view, with the three teeth almost parallel to one another ; the median tooth connected with the shaft by a long, narrow furrow. The total length of the spicule is about 0.04 mm. and the shaft is about 0.004 mm. in diameter.

(4) Small, semi-bipocillate anisochelæ (Pl. 26. fig. 12 *d*) ; mostly in rosettes ; measuring about 0.01 mm. in length ; the free end of the markedly curved shaft is expanded into a flat, saucer-shaped fimbria ; in front view this appears as a narrow, slightly curved cross beam at the outer end of the shaft ; the fixed end is quadrilateral and of the chelate type. This form of microscle is probably intermediate between an anisochela and a bipocillate.

(5) Small, palmate anisochelæ of the Iophon type (Pl. 26. fig. 12 *e*) ; with only a very minute spur at the small end ; these occur scattered singly and are not so abundant as the other microscleres : length about 0.017 mm.

This sponge appears to be almost identical with *Pseudoesperia enigmatica* (olim *Esperia parasitica* Carter [1880]) except for the absence of sandy fibre so characteristic of Carter's specimens. We have examined a microscopic preparation of Carter's type-specimen (?) in the British Museum collection, and find that the small, semi-bipocillate anisochelæ are certainly present, though not mentioned in his description.

*Register No. and Locality.* II. 15, Wooded Isle.

### 33. *PSEUDOESPERIA TRICHOPHORA* n. sp.

The single specimen consists of a small, light-brown fragment encrusting a *Hircinia* sp. ?

The main skeleton consists of a reticulation of stout, ill-defined spicular fibre with many loose megascleres scattered irregularly ; radially arranged brushes of tylostyles lie vertically to the surface.

The spiculation agrees closely with that of *Pseudoesperia carteri*, except that the sigmata are entirely replaced by trichodragmata.

*Spicules* :—(1) Tylostyli ; size about 0·34 by 0·006 mm.

(2) Large, quadridentate anisochelæ ; about 0·056 mm. in length.

(3) Small, semi-bipocillate anisochelæ, about 0·01 mm. in length.

(4) Small, palmate anisochelæ, about 0·012 mm. in length.

(5) Trichodragmata ; short, compact bundles, measuring about 0·026 by 0·006 mm.

It is an interesting fact that this species differs from *Pseudoesperia carteri* only in the replacement of the sigmata of the former by trichodragmata. These spicules are so widely and sporadically distributed throughout the tetraxonid sponges that it is extremely difficult to estimate their taxonomic value.

The peculiar form of the quadridentate anisochelæ and the occurrence of what we have called the “semi-bipocillates” seem to justify the retention of Carter’s genus *Pseudoesperia*.

*Register No. and Locality.* II. 12 a, Wooded Isle.

### 34. *ESPERELLA PLUMOSA* (Carter).

(For literature and synonymy *vide* Dendy [1916 A].)

The material consists of a small, whitish-yellow fragment encrusting *Hippospongia intestinalis* (Lamarck). No further description is necessary.

*Previously known Distribution.* Mauritius and Mergui Archipelago (Carter); Ceylon, Okhamandal (Dendy).

*Register No. and Locality.* VI. 13 b, Sandy Isle.

### 35. *BIEMNA TUBULATA* Dendy.

*Desmacella tubulata* Dendy [1905, 1916 A].

*Biemna microza* Hentschel [1911].

*Toxemma tubulata* Hallmann [1917].

*Biemna tubulata* Dendy [1921 B].

The material consists of a couple of fragments of thin-walled tubes, the outer surface of which appears slightly granular, while the inner bears numerous minute openings of exhalant canals. Colour in spirit brownish yellow ; texture very soft and fragile.

The skeleton arrangement and spiculation agree very closely with those of previously described specimens.

We consider *Biemna microza* Hentschel [1911] to be identical with this species.

*Previously known Distribution.* Gulf of Manaar, Okhamandal, Indian Ocean (Dendy) ; S.W. Australia (Hentschel).

*Register No. and Locality.* VIII. 3, Sandy Isle.

36. *ECHINODICTYUM BILAMELLATUM* (Lamarck) Ridley.*Spongia bilamellata* Lamarck [1818].*Echinodictyum bilamellatum* Ridley [1881].*Echinonema vasipicata* Carter [1882 B].*Kalykteron elegans* Lendenfeld [1888].*Kalykteron silex* Lendenfeld [1888].*Thalassodendron typica* Whitelegge [1901].*Echinodictyum bilamellatum* Hentschel [1911].*Echinodictyum elegans* Hallman [1912].

There is in the collection one beautiful, cup-shaped specimen, 110 mm. in height, with a short stalk and very slightly folded walls. The colour in spirit of the inner surface is almost black, that of the outside grey merging to violet.

The skeleton arrangement and spiculation agree very closely with those of the specimens described by Ridley and Hentschel.

We have also examined two dry specimens of this species from the Dampier Archipelago, N.W. Australia, which are in Professor Dendy's collection at King's College, London. These are both cup-shaped with much folded walls.

*Previously known Distribution.* N.W. and W. Australia (Ridley); Fremantle, S.W. Australia (Carter); S.W. Australia (Hentschel); E. and W. Australia (Lendenfeld); E. Australia (Whitelegge, Hallmann).

*Register No. and Locality.* V., Albrohlos Islands.

37. *ANCHINOE FICTITIOIDES* n. sp. (Pl. 25. fig. 13; Pl. 26. fig. 13.)

There are two specimens in the collection, each forming an almost continuous, vertical, fan-shaped lamella, with an irregularly indented upper margin. The larger specimen (R.N. VI. 4, Pl. 25. fig. 13), which measures 150 mm. in greatest height, 95 mm. in greatest width, and has an average thickness of 7 mm., has two conspicuous oval fenestræ; the other specimen has only one fenestra. The width of both specimens diminishes gradually below to a narrow base of attachment. The colour of the larger specimen in spirit is pale greyish yellow, that of the smaller light brown; texture fibrous, tough and resilient. The surface is glabrous.

On both surfaces numerous circular, slightly raised, pustule-like, cribriform pore-areas are closely but irregularly scattered. The larger of these pore-areas measure 3 or 4 mm. in diameter; they vary, however, in size, number, and conspicuousness in different parts of the same specimen.

A few small, marginal vents are seen in both specimens. A ramifying and anastomosing system of inhalant and exhalant subdermal canals can be seen through the thin dermal membrane.

In the deeper parts of the sponge the main skeleton consists of an irregular network of horny fibre cored to a varying extent by smooth megascleres (tornotoxea) and ochinated by acanthostyli. Dense fibres, consisting only of tornotoxea, ascend somewhat irregularly towards the surface, and the radially arranged terminal spicules of these fibres form a fringe round

the pore-areas. The sieve-membrane of these areas is free from spicules, except for numerous isochelæ.

*Spicules*:—(1) Tornotoxea (Pl. 26. fig. 13 a); smooth, slender, usually straight; ends hastate but unequal; size about 0.4 by 0.006 mm.

(2) Acanthostyli of two kinds—(a) (Pl. 26. fig. 13 b) with short, straight or sometimes slightly curved shaft, which is slightly swollen at one end and sharply pointed at the other, covered with small, slightly recurved spines; size about 0.14 by 0.013 mm.: (b) (Pl. 26, fig. 13 c) with long, slightly curved shaft, the curve being most noticeable just above the slightly swollen base; the spines are very small and only extend for about two-thirds of the shaft from the base, thus leaving the sharply-pointed apical end quite smooth. These longer acanthostyles, which measure about 0.35 by 0.01 mm., are found only in the larger specimen (R.N. VI. 4).

(3) Tridentate isochelæ (chelæ arcuatæ) (Pl. 26. fig. 13 d), with stout, slightly curved shaft and short teeth; measuring about 0.024 mm. in length. These spicules are very abundant in the dermal membrane, especially in the pore-areas, but occur also scattered through the choanosome.

This species agrees very closely with the European *Anchinoë fictivus* (Bowerbank) J. Stephens [1921] as regards its pore-areas and spiculation, but differs widely in its mode of growth, which closely resembles that of *Yvesia* (*Grayella*) *spinulata* Hentschel [1911], also a S.W. Australian and Indian Ocean species (*vide* Dendy [1921 A]). Indeed, *Yvesia spinulata* differs from *Anchinoë pectinioides* in little if anything more than the replacement of the acanthostyles by acanthoxea, and may probably be regarded as a direct derivative of the latter species.

*Register Nos. and Locality.* VI. 4, VI. 11, Sandy Isle.

### 38. DENDORICELLA SCHMIDTI (Ridley).

*Orella schmidtii* Ridley [1884].

*Damiria australiensis* Dendy [1896].

*Damiria Schmidtii* Topsent [1897].

*Damiria australiensis* Lindgren [1897, 1898].

*Dendoricella Schmidtii* Hentschel [1911, 1912 A].

The larger of the two specimens (R.N. IV. 9) in the collection consists of five erect, digitiform processes springing from a thin, common base; the processes measure about 8 mm. in diameter, and four of them divide at their ends into a varying number of slender, secondary, digitiform processes. The second specimen (R.N. III. 10) consists of a portion of a single lobe, dividing above into four slender, digitiform processes. The general surface of the sponge is covered with narrow, meandering ridges running longitudinally; the dermal membrane, which is smooth and transparent, is interrupted by small pore-sieves, visible with a lens. A number of small oval vents, sometimes lying in slight depressions, are scattered singly on the processes. Colour in spirit light greyish brown; texture very soft, spongy, friable.



The skeleton arrangement and spiculation agree with those of previously described specimens.

*Spicules*:—(1) Oxea; measuring about 0·23 by 0·01 mm.

(2) Amphitylota; some straight, others slightly undulating, measuring about 0·31 by 0·007 mm.

(3) C-shaped sigmata of two sizes, the larger measuring about 0·039 by 0·0028 mm., the smaller 0·02 by 0·0014 mm.

(4) Tridentate isochelæ (chelæ arcuatæ) of two sizes, the larger being about 0·034 mm. and the smaller about 0·022 mm. in length.

*Previously known Distribution.* Port Jackson (*Ridley*); Port Phillip Heads (*Dendy*); Amboina (*Topsent*); S.W. Australia (*Hentschel*).

*Register Nos. and Locality.* III. 10, IV. 9, Wooded Isle.

### 39. *TRACHYCLADUS LÆVISPIRULIFER* Carter.

*Trachycladus lævispirulifer* Carter [1879, 1885-6].

*Trachycladus lævispirulifer* Dendy [1897].

(For further possible synonymy see Hallmann's species [1916].)

The external form of the single specimen resembles closely that of *Trachycladus digitatus* var. *clavatus* Hallmann [1916]. The branches, which anastomose freely, are subcylindrical, and their surface appears minutely conulose owing to the up-pushing of the dermal membrane by the ends of the impinging skeleton fibres. The inhalant pores are scattered singly, closely and for the most part equidistantly over the entire surface, giving it a minutely reticulate appearance. The small oscula are scattered sparsely and irregularly. Colour in spirit whitish brown; texture tough and dense.

The skeleton arrangement calls for no comment.

*Spicules*:—(1) Oxea; smooth, curved, of nearly uniform diameter throughout their length, bluntly pointed, measuring about 0·47 by 0·016 mm.; very rarely stylote.

(2) Spinispiræ; minutely spined, corkscrew spicules, usually of two complete turns, measuring about 0·0135 mm. in length; very abundant. Simpler forms, C- and S-shaped, are found frequently.

(3) Microstrongyla; of two kinds—(a) slender, centrotylote, 0·019 mm. long; (b) stout, rarely centrotylote, 0·016 by 0·003 mm. These microscleres are rare.

We have examined preparations of this species in Mr. Carter's own cabinet, and feel justified in identifying with it the Abrolhos specimen, although the oxea of the latter are larger and the microstrongyla less abundant.

Hallmann [1916] has endeavoured to distinguish between a number of Australian species, some of which he describes as new. We are inclined to think, however, that the differences between Hallmann's specimens are not sufficiently great to justify specific distinction being made, and that probably

all the known Australian specimens of *Trachycladus*, as well as Lendenfeld's *Spirophora digitata* and *Spirophora bacterium*, should be included in *Trachycladus laevispirulifer* Carter.

*Previously known Distribution.* South-West Australia (Carter); Port Phillip Heads, Australia (Dendy).

*Register No. and Locality.* III. 9, Wooded Isle.

40. SIGMOSCEPTRELLA FIBROSA Dendy. (Pl. 25. fig. 14.)

*Spirastrella fibrosa* Dendy [1897].

*Sigmosceptrella fibrosa* Dendy [1921 A].

The single fine specimen in the collection, which measures 70 mm. in height, is sessile and lobodigitate. Surface sub-glabrous, almost smooth in parts, slightly conulose or nodular in others. The close-set inhalant pore-areas give the surface a minutely reticulate appearance. They overlie large, funnel-shaped chones in the cortex, which is slightly fibrous and measures up to 0.4 mm. in thickness. The roof of each chone is not merely a dermal membrane, but is moderately thick, strengthened by microscleres (sigmodiscorhabds), and pierced by individual pores which take the form of short canals. The lower part of the chone is constricted to a relatively small opening, which leads into a spacious subcortical crypt: from this, inhalant canals, provided with diaphragms along their length, penetrate the choanosome. The canal system is eurypylous, the flagellate chambers spherical and measuring up to 0.05 mm. in diameter. The larger exhalant canals and the wide oscular tubes are surrounded by a thick layer of gelatinous mesogloea. Vents small but prominent, scattered singly on the upper margin of the sponge, sometimes at the ends of small conical projections. Each vent is much smaller than the diameter of the oscular tube out of which it opens, so that the latter appears to have a thin roof with the vent in the middle. Colour in spirit yellowish white; texture firm, compact, resilient.

The skeleton arrangement agrees closely with Dendy's original description. Between the chones the cortex is packed with microscleres, intermingled in places with the ends of the radial bundles of megascleres.

*Spicules*:—(1) Styli; straight, evenly rounded or slightly enlarged at the base and sharply pointed at the apex, very uniform in shape and size, measuring about 0.34 by 0.01 mm.

(2) Isodiscorhabds (sigmodiscorhabds); measuring in total length about 0.05 mm.; the diameter of the smooth shaft is about 0.008 mm., that of a whorl with the spines included 0.025 mm. The development and adult form of these spicules have been described and figured by Dendy in "The Tetraxonid Sponge Spicule—A Study in Evolution" [1921 A].

*Previously known Distribution.* Port Phillip Heads (Dendy).

*Register No. and Locality.* VI. 2, Sandy Isle.

41. *SPIRASTRELLA VAGABUNDA* *Ridley*.*Spirastrella vagabunda* Ridley [1884].(For literature and possible synonymy *vide* Dendy [1905] and Vosmaer [1911].)

The larger of the two specimens, which measures about 60 by 20 by 25 mm., is elongated and tubular, with a hollow digitiform process (which has been cut off) arising from one end. Two large, irregularly shaped vents are present, and inhalant pores-sieves are visible over a small portion of the smooth but uneven surface. The second specimen is a small tubular fragment with thick walls. Colour in spirit light brown; texture firm and compact.

The skeleton arrangement and spiculation agree closely with those of the type.

The Abrolhos specimens come very close to *Spirastrella vagabunda* var. *tubulodigitata* Dendy [1905], but the tylostyles of the former are shorter and stouter.

*Previously known Distribution.* Torres Straits (*Ridley*); Indian Ocean (*Dendy*).

*Register Nos. and Locality.* VI. 10, VI. 15 a, Sandy Isle.

42. *ΑΑΡΤΟΣ ΑΑΡΤΟΣ* (*Schmidt*).*Ancorina aptos* O. Schmidt [1864].*Aptos adriatica* Gray [1867].*Ancorina aptos* O. Schmidt [1868].*Trachya pernucleata* Carter [1870].*Tuberella tethyoides* Keller [1880].*Tethyophæna slyfica* O. Schmidt [1880].*Tuberella tethyoides* Vosmaer [1887].*Aptos adriatica* Vosmaer [1887].*Amorphina Duchassaingii* Topsent [1888].*Suberites apissus* Topsent [1892].*Tuberella Duchassaingii* Topsent [1894].*Tuberella tethyoides* Topsent [1896].*Suberites aptus* Lendenfeld [1896].*Suberites aptus* Topsent [1898].*Tuberella aptos* Topsent [1898, 1900].*Tuberella aptos* Wilson [1902].*Tuberella aptos* Hentschel [1909, 1912].*Tuberella aptos* Dendy [1916 A].*Tuberella aptos* Babié [1922].

The larger of the two specimens (R.N. III. 5) is irregularly subspherical, measuring 45 by 25 by 30 mm.; at one end, in a slight depression, lies a small group of oscula, and three or four small round oscula are scattered singly over the sub-glabrous upper surface. Colour in spirit dark brown outside, light brown inside; texture compact but compressible.

The other specimen (R.N. VI. 12 b) is a small, light-brown fragment 25 mm. in length, 15 mm. in breadth, and 8 mm. in thickness, with a flat, sub-glabrous upper surface, in the centre of which is a single slit-like

osculum raised on a small papilla. Pigment granules are present in the large specimen, absent in the small one.

The skeleton arrangement and spiculation agree closely with the descriptions given by Topsent and Wilson.

We propose to revive here Gray's generic name *Aaptos* [1867], because we can find no adequate reason why Keller's genus *Tuberella* [1880] should stand in place of it, though we regard his species *Tuberella tethyoides* as synonymous with *Ancorina aaptos* Schmidt. We have revised and brought up to date Topsent's synonymy list, which we think can be definitely accepted.

Carter [1870] described a new genus and species of sponge under the name *Trachya pernucleata*; after examining his preparations we think it justifiable to identify this species with *Aaptos aaptos* (Schmidt), and it is therefore included in the synonymy list.

Carter [1882 A, 1886] described two more species of *Trachya*, viz. *Trachya durissima* and *Trachya horrida*; these are probably identical with his original species, *Trachya pernucleata*.

*Trachya globosa* Carter [1885-86] and *Trachya globosa* var. *rugosa* Carter [1886] are obviously lipotriænose Tetillids, having exceedingly long, slender oxea for megascleres and sigmata for microscleres.

Carter [1876, 1882 A] proposed a group Polymastina in the Sub-order Suberitida to include his genus *Trachya* as well as the typical *Polymastia*, referring to *Trachya pernucleata* and its allies as "*Geodia*-like forms of *Polymastia*."

Although Vosmaer, Topsent and Wilson have placed the genus *Tuberella* (= *Aaptos*) in the Tethyidæ (Donatiidæ), we are inclined to agree more with Carter's views; and so, because of the arrangement of the skeleton, the absence of any fibrous cortex and the presence of pin-head spicules in some cases, we now propose to transfer it to the Sigmatotetraxonida. Family Clavulidæ, Sub-family Suberitinæ.

*Previously known Distribution.* Mediterranean (Schmidt, Lendenfeld, Topsent); Gulf of Naples (Keller); Gulf of Mexico (Topsent); Porto Rico (Wilson); S.W. Australia (Hentschel); Aru Islands (Hentschel); Okhamandal (Dendy).

*Register Nos. and Locality.* III. 5, Wooded Isle; VI. 12 b, Sandy Isle.

#### 43. POLYMASTIA MAMMILLARIS (O. F. Müller) Bowerbank.

(For literature and synonymy *vide* Topsent [1900].)

There is a single small specimen, consisting of about six smooth, slender, thin-walled, hollow, mammiform projections, 10 to 15 mm. in length, rising from a plate-like base which has either been torn off a stone or from a larger specimen; the surface of the base is slightly hispid. The colour in spirit is dull brown owing to the development of pigment granules.

The skeleton arrangement and spiculation agree with the descriptions given by Bowerbank and Topsent.

*Spicules*:—(1) Small tylostyles ; size about 0·17 by 0·008 mm.

(2) Large tylostyles ; size about 1·1 by 0·02 mm. ; the size of the head varies greatly.

*Previously known Distribution.* Cosmopolitan.

*Register No. and Locality.* VI. 12 d, Sandy Isle.

44. *MEGALOPASTAS ARENIFIBROSA* n. sp. (Pl. 25. fig. 15.)

There are three specimens of this sponge in the collection. The largest (R.N. VI. 3, Pl. 25. fig. 15), which must be regarded as the type of the species, is sessile, erect, and consists of a principal lamella giving off a number of secondary lamellae of varying size. The specimen is 110 mm. high and 70 mm. wide, and the thickness of the lamella is about 3 mm. The second specimen (R.N. VI. 9), which is 65 mm. high, 15 mm. wide and about 5 mm. thick, is a fragment probably broken off the type. The third specimen (R.N. IV. 4) is small and lamino-clathrous, becoming constricted towards the base of attachment. The total height is about 50 mm., the maximum breadth about 55 mm., and the average thickness of the lamella about 4 mm. The surface appears granulated, the granules being really numerous, minute, close-set conuli. The vents are small, round and single ; some are arranged marginally, others are scattered, but almost always confined to one surface of each lamella. Colour in spirit dark brown, becoming lighter towards the base of the sponge ; texture compressible, resilient, fairly tough.

The main skeleton consists of primary fibres, about 0·09 mm. in diameter, running vertically to the surface and connected by an irregular network of secondary fibres about half the diameter of the primaries ; the outermost of the secondary fibres form a distinct subdermal skeleton network, the fibres averaging about 0·03 mm. in diameter. The fibres are laminated and "pithed" and the primary fibres are cored by numerous sand-grains and broken spicules.

The dermal membrane, which sometimes contains a good many broken spicules, is pierced by round inhalant pores, about 0·06 mm. in diameter, which lead into large subdermal cavities lying in the ectosome, which contains numerous close-packed, granular, stellate cells. The canal-system is lacunar ; the flagellate chambers, which are large, sac-shaped, averaging about 0·05 mm. in diameter, are placed fairly close together and are eurypylous. The mesogloea of the choanosome is not strongly developed, except around some of the larger canals, where it is collenchymatous, with stellate cells. There are also numerous bands of fibrous tissue, composed of granular, elongated cells, running in from the ectosome in places and deeply penetrating the choanosome.

This species is well characterised by its external appearance and unusually

compact texture, and, above all, by the coring of the primary fibres by sand-grains, which indicates an approach to the Family Spongiidæ.

*Register Nos. and Localities.* VI. 3, VI. 9, Sandy Isle ; IV. 4, Wooded Isle.

45. *SPONGELIA DAKINI* n. sp. (Pl. 25. fig. 11.)

This most interesting specimen forms a very smooth encrustation (about 0.65 mm. thick), almost white in colour, over a considerable portion of the surface of a very fine specimen of *Ancorina australiensis* (Pl. 25. fig. 11).

There is a well-developed, minutely reticulate cortex, about 0.085 mm. thick, formed of sand and broken spicules, which gives the surface a very uniform appearance and presumably covers the vents, as these are not visible.

The main skeleton consists of columns of broken foreign spicules of various kinds, but without visible spongin ; the columns run vertically and sometimes appear to branch slightly as they approach the surface.

The thin, transparent dermal membrane is pierced by numerous round inhalant pores, which measure up to 0.05 mm. in diameter ; usually there is only a single pore in each mesh of the cortex. Small subdermal cavities in the sand cortex lead into large subcortical crypts or inhalant canals in the choanosome, the mesogloea of which is but feebly developed. The flagellate chambers are crowded together, sac-shaped, measuring about 0.06 mm. in diameter ; they are eurypylous and each has several prosopyles. Some of the larger canals appear to be surrounded by fibrous tissue ; these are probably exhalant.

This species is at once distinguished by its thin, encrusting habit and its well-developed, reticulate sand cortex.

*Register No. and Locality.* VI. 6 b, Sandy Isle.

46. *PSAMMOPEMMA CRASSUM* (Carter) var.

*Holopsamma crassa* Carter [1885-6].

*Psammopemma crassum* Lendenfeld [1889].

The single specimen, which is 35 mm. in height, 20 mm. in width, and about 5 mm. in thickness, is erect, somewhat lamellar in shape, thickening considerably towards the base of attachment. The surface is uneven and sometimes rugose. Oscula are not visible. Colour in spirit light greyish brown ; texture hard, gritty, incompressible, but friable.

There is a thin, pore-bearing dermal membrane, overlying large subdermal cavities in the ectosome, which is feebly developed, with collenchymatous mesogloea. The canal-system is lacunar ; the chambers, which have several prosopyles, are large, sac-shaped, measuring about 0.1 mm. in longer diameter, and eurypylous. The gelatinous mesogloea is fairly conspicuous ; it contains stellate cells and also bands of fibrous tissue.

The skeleton consists of a dense mass of sand-grains and broken spicules with no recognisable spongin, interrupted by irregular patches of soft tissue more or less free from sand.

The large size of the flagellate chambers, and the highly lacunar character of the canal-system generally, indicate that this sponge is a true Spongeliid and not a reduced Tetraxonid that has lost its proper spicules.

*Previously known Distribution.* Port Phillip Heads (*Carter, Lendenfeld*); Port Jackson (*Lendenfeld*).

*Register No. and Locality.* IV. 11, Wooded Isle.

#### 47. HIPPOSPONGIA INTESTINALIS (*Lamarck*).

(For literature and synonymy *vide* Dendy [1905].)

There are two specimens in the collection, light brown in colour, of elongated tubular form, with their walls perforated at irregular intervals and the surface slightly conulose. The tubes are about 12 mm. in diameter.

The main skeleton is composed of an irregular network of fairly stout, amber-coloured, horny fibre, the fibres measuring up to 0.08 mm. in diameter. There is a surface reticulation of more slender horny fibre. A certain amount of foreign matter, including a few huge oxeote spicules, has been incorporated within the sponge.

*Previously known Distribution.* Mediterranean (*Lamarck*); Zanzibar (*Hyatt*); Mascarene Islands and Amirante Group (*Ridlen*); Ceylon Seas (*Dendy*).

*Register Nos. and Locality.* VI. 13 a, VII. 2, Sandy Isle.

#### 48. COSCINODERMA PYRIFORME *Lendenfeld* var. *a*.

*Coscinoderma pyriforme* Lendenfeld [1889].

There are four specimens in the collection. The largest (R.N. III. 7), which must be regarded as the type of the variety, is erect, massive, somewhat compressed laterally, and has evidently been attached to a rock along its base and a portion of one side; the total height is 50 mm., the maximum breadth 65 mm., and the average thickness 25 mm. A number of sphinctrate oscula, about 3 mm. in diameter, are arranged along a crest on the upper surface. The second specimen (R.N. II. 7 a), which measures 45 mm. long, 35 mm. wide, and has an average thickness of 12 mm., is oval and somewhat cushion-shaped; a number of round sphinctrate oscula, the largest of which measures 2 mm. in diameter, lie round the edge of the convex upper surface. The under surface is smooth and slightly concave, and has a few small oscula scattered over it. The third specimen (R.N. VI. 20 a) is erect, flabellate, with oval outline, attached to a rock by a short, thick stem; it is 35 mm. high, 28 mm. wide, and about 6 mm. thick; there is a single osculum on one side. The fourth specimen (R.N. VI. 22) is a small oval fragment which has probably been torn off a larger one.

The surface is for the most part minutely conulose, the conuli being more marked in some places than others, while in parts it is quite smooth; there

are also narrow meandering grooves, covered in life by the thin dermal membrane. Colour in spirit-purplish brown in parts, lighter brown in others; texture compact and compressible, resilient, but tough.

There is a thin but well-developed cortex of sand and broken spicules; this cortex is usually of a minutely reticulate nature, the meshes being about 0.13 mm. in diameter and containing inhalant pore-areas. In other parts the cortex seems continuous.

The skeleton consists of primary fibres about 0.05 mm. in diameter, running vertically to the surface and containing much foreign matter (broken spicules); the secondary connecting fibres, which average about 0.02 mm. in diameter, form a close network with somewhat irregular, polygonal meshes about 0.2 mm. wide.

There is a very well developed collenchymatous ectosome, in which lie large subdermal cavities. The canal system resembles closely that of *Euspongia*. Some of the larger canals in the choanosome are surrounded by a thick layer of collenchyma. The flagellate chambers are small, subspherical, and about 0.03 mm. in diameter; they are either eurypylous or with very short canaliculi, and closely packed together. The mesogloea between them is very finely granular. Embryos are present, some in an advanced state of development.

Hyatt [1877] described two sponges, *Spongelia incerta* and *Spongelia spinosa*, which Lendenfeld [1889] makes synonymous with his *Coscinoderma pyriforme*. We can find nothing in Hyatt's description to justify this.

*Register Nos. and Localities.* II. 7 a, III. 7, Wooded Isle; VI. 20 a, VI. 22, Sandy Isle.

#### 48 a. COSCINODERMA PYRIFORME Lendenfeld, var. $\beta$ .

*Coscinoderma pyriforme* Lendenfeld [1889].

The single specimen, which measures 25 mm. in greatest height, 55 mm. in greatest width, and has an average thickness of 10 mm., is a flattened, cup-shaped sponge with irregular but entire margin; it has probably been attached to a rock at several points on its convex lower surface. Colour in spirit dark brown on the upper surface, greyish brown on the lower; texture fine, compact, compressible.

The upper surface is very minutely conulose, subglabrous, and has a well-marked but thin, minutely reticulate cortex made up mostly of broken spicules. Inhalant pore-areas lie in the meshes of the cortex. There are no visible oscula on this surface. The lower surface is smooth and has a thin, continuous cortex formed of broken spicules, no inhalant pore-areas being visible; a number of closed oscula are scattered over this surface, surrounded by radiating subdermal exhalant canals.

The skeleton arrangement and the structure of the soft tissues agree closely with those of *Coscinoderma pyriforme* var.  $\alpha$ . A large number of small,



darkly staining, spherical cells, about 0·006 mm. in diameter, are found embedded in the mesogloea; these cells are most abundant around the various parts of the inhalant canal-system and congregated in immense numbers in the inner portion of the ectosome; they are probably symbiotic algae such as are known to occur frequently in sponges.

*Register No. and Locality.* IV. 5, Wooded Isle.

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## EXPLANATION OF THE PLATES.

## PLATE 25.

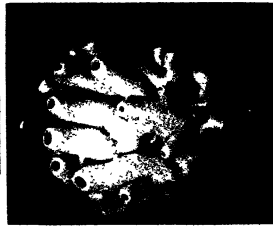
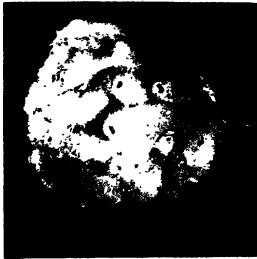
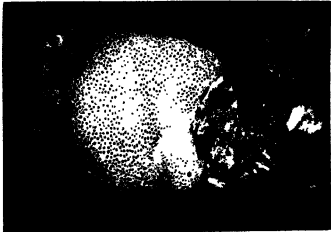
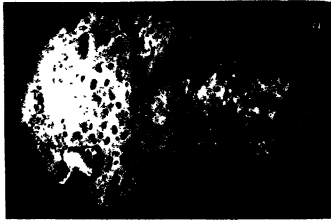
(All the figures in this plate are from photographs)

- Fig. 1. *Leucosolenia grisea* n. sp. R.N. VI. 21.  $\times 1\frac{1}{2}$ .  
 2. *Leucosolenia protogenes* Hæckel. R.N. VIII. 4.  $\times 2$ .  
 3. *Ascoleucetta compressa* n. sp. R.N. III. 12.  $\times 2$ .  
 4. *Tosmaropsis mackinnoni* n. sp. R.N. IV. 1.  $\times 1\frac{1}{2}$ .  
 5. *Grantiopsis cylindrica* Dendy. R.N. VII. 1 a.  $\times 3\frac{1}{2}$ .  
 6. *Grantiopsis cylindrica* Dendy. R.N. VII. 1 b.  $\times 3$ .  
 7. *Grantiopsis cylindrica* Dendy. R.N. VI. 17 c.  $\times 2$ .  
 8. *Grantiopsis cylindrica* Dendy. R.N. I. 1.  $\times 2$ .  
 9. *Grantiopsis cylindrica* Dendy var. *fruticosa* nov. R.N. III. 4  $\times 2$ .  
 10. *Lelapia antiqua* n. sp. R.N. VII. 1 c.  $\times 2\frac{1}{2}$ .  
 11. *Ancorina australiensis* Carter. R.N. VI. 6 a; encrusted by *Spongelia dakini* n. sp., R.N. VI. 6 b.  $\times 1$ .  
 12. *Reniera aqueductus* Schmidt. R.N. VII. 3.  $\times 1$ .  
 13. *Anchinus fletitioides* n. sp. R.N. VI. 1.  $\times 1$ .  
 14. *Signosceptrella fibrosa* Dendy. R.N. VI. 2  $\times \frac{1}{2}$ .  
 15. *Megalopastas arenifibrosa* n. sp. R.N. VI. 3.  $\times \frac{1}{4}$ .

## PLATE 26.

- Fig. 1. *Leucosolenia grisea* n. sp. R.N. VI. 21.  
 a. Triradiates,  $\times 150$ ; b. Quadriradiates,  $\times 150$ .  
 Fig. 2. *Ascoleucetta compressa* n. sp. R.N. III. 12.  
 a. Large triradiates,  $\times 60$ ; b. Small triradiates,  $\times 150$ ; c-c. Quadriradiates,  $\times 150$ .  
 Fig. 3. *Ascoleucetta compressa* n. sp. R.N. III. 12. Diagrammatic vertical section through margin, showing canal-system.  $\times 20$ .  
*i.a.*, inhalant apertures; *d.cor.*, dermal cortex; *i.c.*, inhalant canal; *fl.ch.*, flagellate chamber; *e.a.o.*, exhalant opening of chamber; *e.c.*, exhalant canal; *osc.*, oeculum; *mes.*, mesoglea.  
 Fig. 4. *Ascoleucetta compressa* n. sp. R.N. III. 12. Portion of similar section.  $\times 60$ .  
*c.c.*, collared cells; *pr.*, prosopyle; *tr.*, large triradiates of dermal cortex (*d.c.*); *a.r.*, apical rays of quadriradiates projecting into flagellate chamber and exhalant canal. Other lettering as before.  
 Fig. 5. *Ascoleucetta compressa* n. sp. R.N. III. 12. Dermal surface, showing skeleton arrangement round inhalant aperture,  $\times 100$ .  
*tr.*, trichoxea.  
 Fig. 6. *Tosmaropsis mackinnoni* n. sp. R.N. VI. 1.  
 a. Large oxea,  $\times 40$ ; b. Subgastral or tubar sagittal triradiates,  $\times 40$ ; c. Subdermal pseudo-sagittal triradiates,  $\times 40$ ; d. Triradiates of the dermal cortex,  $\times 40$ ; e. Triradiates of the gastral cortex,  $\times 40$ .  
 Fig. 7. *Grantiopsis cylindrica* Dendy. R.N. I. 1.  
 a. Triradiates of dermal cortex,  $\times 60$ ; b. Dermal microxea,  $\times 150$ ; c. Subgastral quadriradiates,  $\times 150$ ; d. Reduced tubar triradiates,  $\times 150$ ; e. Head of tubar triradiates, showing the two vestigial rays,  $\times 950$ ; f. Gastral quadriradiates,  $\times 150$ ; a.r. apical ray; g. Oxsets from ocular fringe,  $\times 150$ ; h. Ocular triradiates,  $\times 150$ .





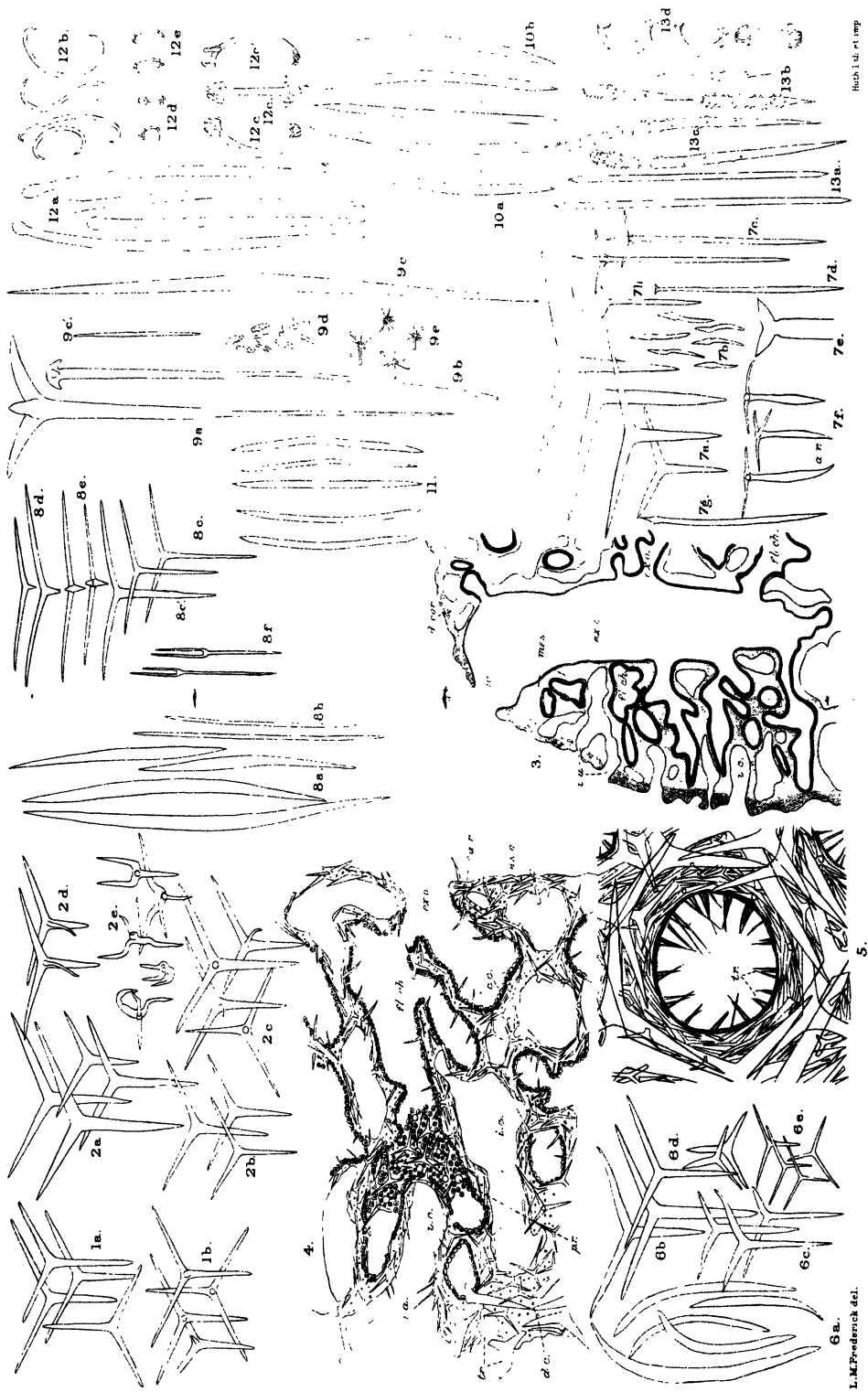
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SPONGES FROM ABROLHOS ISLANDS.









L.M. Frederick del.

Fig. 1. 11. et 12. rep.

SPONGES FROM ABROLHOS ISLANDS.



Fig. 8. *Lelapia antiqua* n. sp. R.N. VII. 1 c.

a. Large oxea,  $\times 40$ ; b. Slender oxea from dermal brushes,  $\times 40$ ; c. Normal sagittal triradiates of dermal cortex,  $\times 60$ ; c'. Subgastral sagittal triradiate,  $\times 60$ ; d. Alate triradiates of gastral cortex,  $\times 60$ ; e. Alate quadriradiates of peristome,  $\times 60$ ; f. "Tuning-fork" spicules,  $\times 60$ .

Fig. 9. *Ancorina brevidens* n. sp. R.N. VI. 16 b.

a. Orthotriæne,  $\times 100$ ; b. Anatriæne,  $\times 100$ ; c. Large oxeote,  $\times 100$ ; c'. Small ectosomal oxeote,  $\times 100$ ; d. Microrhabds,  $\times 360$ ; e. Tylasters,  $\times 360$ .

Fig. 10. *Halichondria phakellioides* n. sp. R.N. VI. 1.

a. Oxea,  $\times 100$ ; b. Stylote,  $\times 100$ .

Fig. 11. *Phlæodictyon abrolhosensis* n. sp. R.N. II. 9.

Oxea,  $\times 190$ .

Fig. 12. *Pseudoesperia carteri* n. sp. R.N. II. 15.

a. Tylostyli,  $\times 270$ ; b. Sigmata,  $\times 550$ ; c. Quadridentate anisochela, side view,  $\times 550$ ; c'. Quadridentate anisochela, face view seen from the back,  $\times 550$ ; c''. Young quadridentate anisochela, side view,  $\times 550$ ; d. Small semi-bipocillate anisochelæ,  $\times 550$ ; e. Small palmate anisochelæ,  $\times 550$ .

Fig. 13. *Anchinoë fictitioides* n. sp. R.N. VI. 4.

a. Tornotoxea,  $\times 190$ ; b. Small acanthostyli,  $\times 190$ ; c. Long acanthostyli,  $\times 190$ ; d. Tridentate anisochelæ (chele arcuatæ),  $\times 650$ .



**Report on Opisthobranchiata from the Abrolhos Islands, Western Australia, with Description of a new parasitic Copepod.** By CHAS. H. O'DONOGHUE, D.Sc., F.R.S.C., Professor of Zoology, University of Manitoba, Canada. (Communicated by Prof. W. J. DAKIN, D.Sc., F.L.S.)

[Percy Sladen Trust Expedition to the Abrolhos Islands  
under the leadership of Prof. W. J. DAKIN.]

(PLATES 27-30.)

[Read 21st June, 1923.]

FROM a very cursory examination of the distribution of the Opisthobranchs, it is evident that the Indian Ocean is very rich in members of this group and is characterized particularly by certain genera. For this reason we may look forward to the coasts of Australia furnishing a large number of interesting forms. Up to the present, however, they have not been studied in this area with any degree of thoroughness, save in the neighbourhood of Sydney by Angus (7) and less extensively in South Australia by Basedow and Hedley (8). In Western Australia it may be said that no systematic collecting has been done, so that our knowledge of the Opisthobranch fauna of this coast is very limited.

The present collection, while small in numbers, is, nevertheless, interesting and, it is to be hoped, useful. Certain of the species themselves appear to be new, and some of the others, although previously recorded, have only been incompletely described, so that it has been possible in all cases to give here further essential information regarding their structure or distribution and to clear up certain doubtful points. In these ways therefore it will extend our hitherto meagre knowledge of Western Australian forms and so help to fill a noticeable gap.

The student of the Opisthobranchiata, and especially the Nudibranchiata, is generally faced with one of two very serious difficulties. On the one hand, if he collects living material, he does not as a rule have the opportunity to dissect it and, more particularly, to examine the radula. On the other hand, if he is working out a collection in a museum or laboratory, while he is able to make such dissections and preparations of the radulae as the material allows, he is usually not in a position to recognize the original colour, or perhaps even shape, of the living creature. I doubt if any other group of animals is so disappointing when preserved; anyone used to seeing them alive, with their beautiful coloration and often graceful shape, would hardly recognize them in the shrivelled discoloured lumps that they become after preservation. Hence it follows that unless the two aspects are dealt

with simultaneously, there is always the possibility of one species receiving two different names, one from the collector who knows the living animal and the other from the laboratory worker who has handled only preserved material—indeed, it would not be difficult to cite instances of this. That this may occur in Australian material is made possible in the case of the paper by G. F. Angas on the Nudibranchs of New South Wales (7). This work is illustrated by a number of excellent coloured figures, from which I should judge a collector would have practically no difficulty in recognizing the living forms at once. As no details or figures of the radulæ or other internal organs are given, however, it would be impossible to recognize a number of the species from a collection of preserved material without colour-notes.

This difficulty may be overcome if the same person works at the forms from the two aspects, or by the co-operation of two individuals. In the present case I have been fortunate enough to look through the collection with Professor Dakin, who gave me colour-notes, which, while brief, should be sufficient to allow of the easy recognition of the living animal. In two instances he supplied me with coloured drawings.

It has already been noted that the Opisthobranchs of Australia are but little known, and they would well repay further study, but it is of the utmost importance that when collections are being made adequate colour-notes of the living animal should be taken.

The list of workers who have treated of West Australian forms is very limited. The earliest records are those of Cuvier, 1804 (31), who described two species of Nudibranchs brought back by Péron from that coast. Quoy and Gaimard in 1833 (68) described one further species. Sowerby in 1869 (71) described the shell of a Tectibranch from the Cuming collection in the British Museum. In 1876 Abraham (1) described another Nudibranch from the British Museum material, and Bergh (12) one from the Cuming collection in the British Museum. A species brought back by Dr. Studer in the 'Gazelle' was described by Bergh in 1880 (22). Kent (54) in 1897 recorded a single species that actually came from the Abrolhos Islands. Lastly, in 1917 Odhner (59) described three further Nudibranchs which were brought back by Dr. Mjöberg's Swedish scientific expeditions to Australia in 1910-13.

The species recorded therefore are :—

#### **TECTIBRANCHIATA.**

*Tethys* [*Aplysia gigantea*] (Sowerby), recorded from Swan River.

#### **NUDIBRANCHIATA.**

##### **GLADOHEPATICA.**

*Scyllaea pelagica* Linn., recorded by Cuvier from Terre d'Edels.

*Phyllirhoë lichtensteinii* Eschscholtz, recorded by Quoy and Gaimard from Terre d'Edels.

*Armina (Pleurophyllidia) cygnea* (Bergh), recorded from Swan River.

*Madrella ferruginosa* Ald. & Hanc., recorded by Odhner from Cape Joubert.

#### HOLOHEPATICA.

*Hexabranhus imperialis* Kent, recorded from the Abrolhos.

*Kentrodoris maculosa* (Cuvier), recorded from Baye des Chiens marins.

*Ceratosoma brevicaudatum* Abraham, recorded from West Australia.

*Ceratosoma corallinum* Odhner, recorded from Cape Joubert.

*Phyllidia varicosa* Bergh, recorded from Dampier's Archipelago.

*Trereyana marginata* Odhner, recorded from Cape Joubert.

This is a small list of only 11 species and the present collection contains 16 species, only three of which have been recorded previously from West Australia, and so the total now known from the coast is 24—a very small number when one considers the length of the coast-line and the fact that there is every indication of its possessing a rich fauna.

The following species are here represented :—

#### TECTIBRANCHIATA.

*Tethys [Aplysia] gigantea* (Sowerby).

*Tethys [Aplysia] denisoni* (Smith).

*Dolabrifera pelsartensis*, sp. nov.

*Berthella plumula* (Montagu).

#### ASCOGLOSSA.

*Placobranhus expansa*, sp. nov.

#### NUDIBRANCHIATA.

##### HOLOHEPATICA.

*Splurostoma [Tritonia] dakini*, sp. nov.

*Hexabranhus imperialis* Kent.

*Alloiodoris hedleyi*, sp. nov.

*Asteronotus fuscus*, sp. nov.

*Glossodoris [Chromodoris] westraliensis*, sp. nov.

*Aphelodoris affinis* Eliot.

*Ceratosoma brevicaudatum* Abraham.

*Dendrodoris [Doriopsis] nigra* (Stimpson).

*Dendrodoris [Doriopsis] mammosa* (Abraham).

*Nembrotha purpureolineata*, sp. nov.

*Notodoris gurdineri* Eliot.

With such a small list it is hardly profitable to spend much time in the discussion of the distribution and relationships of its members, for as soon as any systematic collecting is done the list will be enormously increased.

Professor Dakin has called attention to one or two points in his general description of the expedition (32) that need brief consideration here. In



the first place, the Abrolhos Islands are probably the most southern coral-islands in the world. A tropical current from the north and north-east passes down and bathes their shores, and the available evidence goes to show that the temperature of the sea round the islands is usually some degrees higher than that near the adjacent coast—indeed, even in the winter, it rarely falls below 20° C. He further suggests that if a preponderance of tropical species is found it will probably be due to this warm current, although the fishes apparently are southern forms.

Of the Tectibranchs, one (i. e., *T. gigantea*) has been recorded previously from Queensland. The two genera *Dolabrifera* and *Placobranchus* are, on the whole, distinctive of tropical or sub-tropical seas, while *Berthella* is perhaps more widely distributed.

It may be stated of the Nudibranchs that, as a general rule, the Cladohepatica are characteristic of cool or cold waters, while the Holohepatica characterise warmer regions. It is therefore probably not without significance that all the forms in the present Abrolhos material belong to the Holohepatica. In passing, too, it may be worth while to notice that, of the Cladohepatic genera recorded from the coast of the mainland of Western Australia, i. e., *Armina* (*Pleurophyllidia*), *Scyllca*, and *Madrella*, the two former are of world-wide distribution and the last is a more or less tropical group. All other West Australian forms so recorded are Holohepatic. Turning again to the present material, the Sphærostomids are universally distributed, but practically all the other genera are distinctly those of tropical and sub-tropical seas.

Comparing this list with that of the British coast or of the northern part of the Pacific Coast of North America, the difference is most striking, and it is impossible not to recognize that it is far more sub-tropical in character. Cold-water groups appear to be entirely unrepresented up to the present, and it is hardly possible that, even if found, they will ever outnumber the tropical and sub-tropical genera.

We may conclude, therefore, that, as far as the Opisthobranchs at present known are concerned, the fauna of the Abrolhos Islands is distinctly sub-tropical or tropical in its constitution.

The remarkable way in which the ordinary usages of systematic taxonomy have not merely been ignored but flagrantly violated by many workers on Nudibranchs has created such a series of pitfalls that even with the utmost care it is almost impossible to avoid them all. Among the most obvious of these are examples where species have been given new names, apparently because the author did not like the previous one, and this although the older name has many years' priority, and the identity of the two forms is emphasized. Again, several genera have been combined and a new generic name invented, or the reverse of this may have happened and an old genus split up to make way for two or more new ones, while the original name has been

discarded. It is obvious that, if this sort of procedure goes on unchecked, the ultimate result will be a chaotic muddle, out of which it will be very difficult to find a way. The present author, in conjunction with Iredale (51 a), has spent a great deal of time in an attempt to straighten out the tangle of the synonymy of the British Nudibranchiata, and, as a result, certain fairly widely used generic names have been replaced by less known ones. The very obvious criticism will be made that such changes will cause a certain amount of inconvenience, and it must be admitted at the outset that this is so. On the other hand, a few hours' work in the taxonomy of any group will soon show that this inconvenience is nothing to the deadlocks that arise from the slipshod and incorrect use of names. The common remark that "everyone knows what so-and-so means" is not merely untrue, for the original describer of the species would not know, but it is frequently a flimsy excuse for avoiding the work necessary to justify the employment of a correct terminology. Furthermore, it becomes impossible to discuss such topics as the comparative anatomy, systematic relationship, and distribution of the members of a large group of animals unless one can be more or less certain of the species involved. Wherever changes from the common usage have been made, the reasons for so doing have been briefly given and a synonymy provided.

My friend Professor Dakin handed the collection over to me for examination, and I wish to offer him my sincere thanks not only for so doing but also for giving the colour-notes mentioned above. I also desire to thank the authorities of the British Museum—in particular, Mr. G. C. Robson—for the privilege of working at the Museum, where ready reference to books and specimens greatly facilitated my work: and, lastly, also Professor Dendy, F.R.S., of King's College, London, in whose laboratories the dissections, preparations of the radulæ, and the drawings were made.

All the drawings of teeth were made with the camera lucida from my own preparations. Type-specimens, examples of all the species, and, when present, the radulæ have been deposited in the British Museum.

#### Order **OPISTHOBRANCHIATA** H. Milne-Edwards, 1848.

The **Gastropoda** belonging to the class **Euthyneura** are all hermaphrodite and characterised by the detorsion of their visceral mass and nerve-commissure; in addition, they generally have two pairs of tentacles and exhibit a tendency, sometimes marked, to concentration of the nervous system. They fall fairly naturally into two orders—the Pulmonata, which are adapted for aerial respiration and life on land, and the Opisthobranchiata, which are adapted for aquatic respiration and a marine life. The Opisthobranchs thus come to form a well-defined group: on the other hand, however, the division of this order is not quite so simple.

Certain authorities—*e.g.*, Bergh (14 & 17), von Jhering (52 & 53)—recognise three sub-orders: namely, the **Tectibranchiata**, the **Nudibranchiata**, and the **Ascoglossa**. The last-named sub-order is characterised *inter alia* by the possession of a uniseriate radula with teeth of a special form which, when worn out, are not ejected, but retained in a sac lying at the base of the buccal apparatus [hence **Saccoglossa** von Jhering (52)]. The difficulty in accepting this classification lies in the fact that the **Ascoglossa** undoubtedly contain two separate groups—(1) the **Lophocercidæ** (*Lobiger* and *Lophocercus*), which show certain marked affinities with the **Tectibranchs**, so that by some authorities they are included with them, and (2) the **Hermæidæ**, **Phyllobranchidæ**, **Placobranchidæ**, **Elysiidæ**, and **Limapontiidæ**, which are undoubtedly more nearly related to the **Nudibranchiata**. Eliot (40), to overcome this, places the **Lophocercidæ** with the **Tectibranchs** and the remaining families with the **Nudibranchs**. While this avoids one difficulty it creates another, for it does not sufficiently mark off these **Ascoglossan** forms, which deserve some recognition. Vayssièr (73) includes the **Lophocercidæ** (**Oxynoidæ**) with the **Tectibranchs** and the remaining families he groups as a separate sub-order—the **Ascoglossa**, allied to the **Nudibranchs**. This restricts the application of the term **Ascoglossa** to the forms allied to the **Nudibranchs**, and excludes from it the **Lophocercidæ** which are included under the older and original usage of the term and which are, of course, **Ascoglossan**. Pelseneer (65) has but two orders in the **Opisthobranchs**—the **Tectibranchia** and **Nudibranchia**. The latter he divides into four Tribes, of which the fourth (the **Elysiomorpha**) is identical with the **Ascoglossa** of Vayssièr. While agreeing that the **Elysiomorpha** constitute a group of forms related to the **Nudibranchs**, I cannot accept Pelseneer's view that they are highly specialised **Eolidomorpha**. Indeed, for a number of reasons that need not be entered into here, I am inclined to think that if there is any relationship between the **Elysiomorpha** and **Eolidomorpha** it is the reverse of this, and the former are to be regarded as the more primitive and not the derived group.

The difficulty remains, and further work on the doubtful and transitional forms will be necessary before it can be satisfactorily settled. For the purpose of the present paper it is intended to adopt the classification set forth by Vayssièr in 1885 (73) and to divide the order **Opisthobranchiata** into three sub-orders—namely, the **Tectibranchiata**, the **Ascoglossa**, and the **Nudibranchiata**, using the term **Ascoglossa** in the restricted sense as identical with the **Elysiomorpha** of Pelseneer.

#### Sub-order TECTIBRANCHIATA (Cuvier, 1817.

The **Tectibranchs** are characterised generally by the possession of a lateral or dorso-lateral gill (ctenidium) on the right side, protected by a fold of the mantle; usually a shell, internal or external; a radula, whose used teeth are

discarded. The asymmetrical position of the etenidium involves also a certain asymmetry of the viscera that is not characteristic of the Nudibranchiata.

The main sub-divisions employed here are those suggested by Fischer in 1884 (41) and adopted by Vaysière (74) and Pilsbry (67) among others, and the sub-order is split into three divisions : (1) **Cephalaspidea**, (2) **Anaspidea**, and (3) **Notaspidea**. Three of the species in the collection belong to the second group (the Anaspidea) and fall within the one family (the Tethyidae). The other belongs to the last group, the Notaspidea.

## (2) **TECTIBRANCHIATA ANASPIDEA** Fischer, 1884.

Tectibranchs that lack a fleshy head-shield ; the head possesses two or four folded or split tentacles ; the shell is spiral or plate-like, usually hidden by mantle, and with a posterior terminal nucleus, rarely absent ; the penis is near right anterior tentacle, the female aperture and vas deferens open near gill.

### Family TETHYIDÆ (APLYSIIDÆ).

The animal is elongate ; the shell is in the form of an uncoiled concave plate, almost or entirely hidden, or absent ; the neck and head are narrower than the body, the mouth is a vertical fissure ; the epipodia or pleuropodia are recurved over back, forming two lateral or dorsal lobes enclosing mantle and gill. The genital orifice lies within dorsal slit, communicating by a long furrow with the invertible penis, which lies near the anterior right tentacle ; the mouth is armed with horny jaws ; the multiserial radula possesses similar teeth ; the stomach is armed with cartilaginous nodules ; the anus is situated behind the gill.

The name generally used for the family is Aplysiidae from the generic name *Aplysia*, but Linnaeus in his tenth edition, 1758, uses the term *Tethys* for an animal which he briefly defines and refers to a figure in Rondelet, and this is beyond doubt the ordinary sea-hare usually referred to now as *Aplysia*. Later, in the twelfth edition, 1767, he applies the term *Aplysia* or *Laplysia* to the very same creature, and uses the name *Tethys* for the Nudibranch commonly known as *Tethys himbria*. Pilsbry has dealt fully with this matter (66), and points out, quite correctly, that the term *Tethys* is the proper one for this genus and not applicable to Nudibranchs. He adopts this nomenclature in his monograph (67, p. 59), but strangely enough retains the old family-name Aplysiidae, whereas the family should take its name from the oldest or typical genus of the family. The correct family-name, however, is used by Hedley (50, p. 107), 1918. There is no doubt that Pilsbry was right in making this change, and the genus is *Tethys* with *Aplysia* as a synonym. It is to be regretted that earlier writers did not go back to the original literature, but continued to use the word *Aplysia* and misapply the term *Tethys*.

## Genus TETHYS Linn. 1758.

Type by designation, *T. leporina* Linn. ; *T. limacina* Linn.  
.being unidentifiable.

Synonymy: APLYSIA Linn., 1767, and subsequent authors.

Type, *Laplysia depilans* Linn.

The animal is swollen behind, narrower in front, with rather a long neck and head, bearing folded tentacles and slit rhinophores as is usual in the family ; the latter lie about midway between tentacles and dorsal slit. The pleuropodia arise in front of the middle of the animal's length, are ample, freely mobile, free throughout their length or united for a distance behind. They are functional as swimming-lobes ; their anterior ends are separated. The mantle nearly covers the gill, having a median tube, foramen, or orifice communicating with shell-cavity, and produced behind in a more or less developed lobe or lobes, folded to form an excurrent siphon. The genital orifice lies under the front edge of the mantle, in front of the gill ; an opaline gland is present a short distance behind the genital opening. The foot is well developed. The shell is very thin and membranous with a thin calcareous inner layer ; it is nearly as large as the mantle, concave, with pointed small apex, bears a recurved lamina, and has a concave posterior sinus.

I am aware that it is an extremely difficult matter in certain cases to identify members of the genus *Tethys* by their shells, which are on the whole very similar, but the two following species have been placed under the same names as previously recorded, but poorly described, forms. This has been done because I have had the opportunity to examine the type-material and in neither case have I been able to detect significant differences between the present and the previously described species. Further, the localities are in each instance sufficiently near to make it probable that they fall within the limits of the distribution of the respective species. Literature, moreover, is strewn with *nomina nuda* due to the multiplication of names founded upon unsatisfactory descriptions or without sufficient notice of previous work.

Species TETHYS GIGANTEA (Sowerby), 1869, Conch. Icon. vol. xvii., *Aplysia*, pl. 1, sp. 1, fig. 1 *a* & *b*. (Pl. 27. fig. 1. Pl. 29. figs. 20-22.)

*Body.* The animal is very large, quite justifying its name of *gigantea*, and its body is plump, high, and somewhat egg-shaped. The visceral hump is placed relatively far back in the largest part of the body, which narrows and gets lower as it passes forwards to the cephalic region. The very well-developed pleuropodial lobes arise a short distance behind the rhinophores, are freely and widely separable, and unite posteriorly to form a transverse fold across the hinder end of the body above the short but well-marked caudal prolongation of the foot. The moderately thick mantle is perforated by a small aperture over the centre of the shell. It covers the ctenidium, save for a narrow strip postero-laterally, but more completely than in the

next species. The anal funnel is strongly marked and protrudes between the hinder margins of the pleuropodia on the right side of the middle line. The integument is soft and smooth, but thrown into a series of raised areas of irregular sizes and shapes, separated from one another by deep narrow grooves. The whole animal, more particularly in lateral aspect, presents a very characteristic appearance, recalling to some extent the appearance of crocodile-hide, but, as just noted, it is quite soft.

The opaline gland occupies a well-defined region below the right anterior part of the mantle. It opens to the mantle-cavity by a very distinct, circular or slightly crescentic, single aperture and not by a series of apertures as in *T. punctata*.

*Colour.* The colour of the preserved specimens is a very deep brownish grey with black lines running in many of the cracks, but also forming areas of interlacing tracery under the pleuropodia and in the caudal region. Professor Dakin informs me that in life the animal was of a deep opaque purple-green.

*Dimensions.* The larger specimen measured, in the preserved condition, 15 cm. long by 6.5 cm. wide and 6 cm. high, but of course would have been much larger in life, as all these animals shrink considerably when preserved. Judging from the type-shells named by Sowerby, one of the original specimens must have been at least a half or two-thirds as large again. If we take the estimate made by Eales (33, p. 12) that when preserved *T. punctata* rarely measures "more than a third of its length when alive," and assume it to apply to *T. gigantea*, we see that it is possible that the present species may reach a length of about 60 cm. (say, 2 ft.).

*Head.* The head and neck-region of this form are quite well developed, although noticeably smaller than the body of the animal. The vertical slit-like mouth has a large auriculate tentacle on each side. These cephalic tentacles do not meet in the mid-dorsal line above the mouth, but an extension of each forms a sort of lateral flange passing on each side of the mouth. The postero-dorsal border of each tentacle is rolled, so as to form a very conspicuous groove facing backwards and outwards. Below and completely hidden by the right oral tentacle is the penis.

*Foot.* The foot is well developed, broad, and muscular. It is not sharply marked off from the pleuropodial lobes laterally, and in the larger specimen its surface presents the same "crocodile skin" pattern as the sides of the body. At the anterior end it is separated from the head by a well-marked groove, and it is expanded into large semicircular lobes which meet across the anterior end. This is present in both specimens, but much more marked in the large one, where this frontal expansion of the foot projects laterally almost the width of the head beyond it on each side. The hinder end of the foot has a similar, but much smaller, expanded lobe borne on each side of the caudal prolongation.

*Rhinophores.* The rhinophores, although considerably smaller than the oral tentacles, are very obvious cylindrico-conical structures lying close together in the dorsal region about halfway between the oral tentacles and the beginnings of the pleuropodia. Their terminal portion takes the form of a fairly thin flap folded upon itself so as to produce a deep groove facing laterally.

*Gill or Ctenidium.* The large gill is crescentic in shape and forms a lobate plume. The anterior portion is attached by a wide base along the pallial cavity and the posterior end is free. Just the edge of the hinder portion protrudes from beneath the mantle.

*Shell.* The shell is transparent, very thin and soft, and of a pale horn-yellow colour. The concentric lines of growth are clearly visible. That of the smaller specimen measures 62 mm. by 41 mm. The shell of the larger specimen was considerably larger, but left intact. The largest of the Sowerby shells in the British Museum was 96 mm. by 79 mm., but it is very dry and shrivelled.

*Labial Armature.* The wall at the hinder end of the buccal cavity is lined by a thin semi-transparent cartilage-like membrane; this takes the form of a compressed tube, whose diameter is 9 mm. high and 4 mm. at its widest point and about 5 mm. long. This is strengthened by two flat cushion-shaped bands, 3.25 mm. wide, of a deep brown colour. They almost touch dorsally, but are slightly more widely separated at their ventral ends. Under the microscope it will be seen that these bands are composed of an enormous number of tiny cylindrical rods with rounded ends, closely packed together to form a sort of "pile" as in velvet. In some works these bands are spoken of as "jaws," but this is not a good term, as they cannot be considered as either homologous in structure or analogous in function with the jaws of Nudibranchs.

*Radula.* The radula is very well developed, and in the smaller of the two specimens measured 15.5 mm. long by 14.5 mm. wide. The total number of rows in the radula was from 83-85. The number of teeth in the various rows was as follows: in the first row 5 (*i.e.*, 2.1.2); in the tenth row 15 (*i.e.*, 7.1.7); and in the seventeenth row about 119 (*i.e.*, 59.1.59). The rachidial tooth is large and consists of a basal plate in the form of a trapezium with a deep notch in the middle of the anterior edge and a leaf-shaped blade. The blade has a broad median denticle with 3 or 4 lateral spines increasing in size towards the base and the two lateral smaller denticles each flanked by one or two spines. The bases of the inner pleurals are roughly rhomboidal with curved sides. The blade contains two main denticles, of which the inner is larger and has 5-6 lateral spines. The outer has 3-4 laterals, the basal one being larger than the others. The pleurals increase in size towards the outside, reaching their maximum more than halfway out. Here they are much longer and the two denticles are very large and almost smooth—

they have a very thin crenulated edge along their basal portions. The teeth decrease in size rapidly at the margin, and the last one or two consist of a single elongated basal plate with no spine.

The conspicuous genital aperture is to be found just in front of the anterior edge of the mantle to the right of the middle line. The seminal groove is well marked and passes forward around the outside of the right rhinophore to the penis underneath the right cephalic tentacle.

The anus lies on a fold of the mantle to the right of the middle line behind the visceral hump. In this region the mantle is somewhat thickened and produced to form an anal funnel which projects beyond the pleuropodia.

*Notes.* Two specimens were obtained from near Fremantle (some 250 miles south of the Abrolhos region), and as Sowerby's specimens were also from "Swan River" the present ones can probably be regarded as topotypes.

Species *TETHYS DENISONI* (Smith), Rep. Zool. Coll. 'Alert,' p. 89 (1884). (Pl. 27. fig. 2; Pl. 29. figs. 23-25.)

*Body.* The body is plump, high, and somewhat egg-shaped, being wider at the hinder end than at the front end, and it passes forwards into a narrower head or cephalic region. The visceral hump appears to be thrown rather far back as compared with *T. (Aplysia) punctata*. The pleuropodial lobes arise laterally about as far behind the rhinophores as those are behind the oral tentacles; they are moderately large and freely separable. Posteriorly they unite and form a sort of transverse flange across the hinder end of the body above the caudal prolongation of the foot. The mantle covers the shell, but possesses a small central perforation, and it also largely covers the ctenidium, which is free for a short distance at its postero-lateral end. The anal funnel is well developed. The integument covering the whole animal is very smooth, but thrown into wrinkles.

The opaline gland is a well-defined body lying under the right anterior portion of the mantle and opening to the mantle by a single fairly large pore and not by a series of apertures as in the European *T. punctata*.

*Colour.* When preserved the animals are of a pale greyish white and the wrinkles are often black, very similar to those in *T. gigantea*. Professor Dakin informs me that in life they are of an olive-green colour with some darker mottlings.

*Dimensions.* The largest specimen when preserved measured 6 cm. long by 3 cm. wide and 3.2 cm. high.

*Head.* This may be regarded as including the head and neck. The mouth is terminal and takes the shape of a vertical slit; on each side is a fairly large auriculate tentacle. These pass down on each side of the mouth, and at their upper border are curled round to form a groove directed posteriorly and outwards. They are separated in the mid-dorsal line and show no



tendency to fuse and form a sort of veil as in *T. punctata*. Below and in front of the right oral tentacle lies the penis.

*Foot.* The foot is large and muscular and fairly broad. It is sharply marked off from the head at the anterior end by a groove, and posteriorly it is continued as a sort of tail. The pleuropodia arise as dorsally-directed flaps from the median and postero-lateral region of the foot.

*Rhinophores.* The rhinophores are two sub-conical projections about 12 mm. high, situated near the mid-dorsal line about halfway between the oral tentacles and the front end of the pleuropodia. They are deeply grooved along the terminal portion of their postero-lateral borders.

*Gill or Ctenidium.* The gill is well developed and is a lobate plume of crescentic shape. It is attached by a wide base along the antero-median margin of the pallial cavity, and posteriorly it passes out freely and the tip is exposed to a relatively greater extent than in the preceding species.

*Shell.* The shell is pale yellow, transparent, with concentric lines of growth clearly showing, and it measures 28 mm. by 25 mm. (Smith's specimen measured 30 by 27 mm.—a fairly close approximation). The postero-dorsal umbo lies far back on the visceral mass. On the longer, more arched, left side of the shell lie a ridge and a groove which run parallel with the edge.

*Labial Armature.* The inner parts of the buccal cavity are lined by a thin hyaline layer of cartilaginous consistency. This takes the form of a tube flattened laterally; its internal dimensions are 5.75 mm. high by 1.5 mm. at its widest point and it is about 4 mm. long. It is strengthened by two slightly raised bands 2.5 mm. wide; these almost touch dorsally, but are a little more separated ventrally. As in the preceding species they are composed of an enormous number of tightly packed circular rods.

*Radula.* The radula is well developed and measured 12.5 mm. long by 10.5 mm. wide when spread out on a slide. It is of a deep horn-yellow colour. The number of rows in the radula is about 48 and the number of teeth in the first row 3 (*i. e.*, 1. 1. 1); in the tenth row 45 (*i. e.*, 22. 1. 22); and in the thirty-fifth row about 87 (*i. e.*, 43. 1. 43). The base of the rachidial tooth is roughly trapezoidal, with a deep rounded notch in the middle of the anterior border. The blade is leaf-shaped and relatively larger than in *T. gigantea*. It has a median spine bearing 3-4 lateral denticles and two lateral spines. The first of these has two lateral denticles and the other is smooth. The base of the first pleural tooth is approximately rhomboidal with curved sides; its blade consists of two well-marked spines, the larger on the inside, and each bears a series of from 2-4 flanking denticles. The pleural teeth get larger as they pass outwards, reaching their maximum well over halfway out. The blade becomes elongated and the spines much longer, but they retain their lateral denticles, about 3-5 in number. Finally, near the lateral margin, first the smaller spine disappears and then

the larger, so that the last two or three teeth consist simply of a narrow oval basal plate. All the types of teeth differ from the corresponding ones in *T. gigantea*.

The genital aperture lies a little to the right of the middle line, just under or very slightly in front of the anterior edge of the mantle, and from it the quite distinct seminal groove passes forwards to the penis, which, as noted above, lies just in front of and below the oral tentacle.

The anus is situated at the hinder end of the visceral hump, practically in the mid-dorsal line and a short distance away from the hump, upon a fold of the mantle. In the neighbourhood of the anus the mantle is thickened and projects outwards in the form of a flap, which is coiled round in such a manner as to form a funnel, the anal funnel, which in this species is relatively larger than in *T. punctata*.

*Notes.* In all, five specimens of this species were obtained: two large ones about the same size from Wooded Island, two smaller ones with no exact locality given, and one quite small one from Pelsart Island. Professor Dakin in his paper on the Abrolhos (32, p. 170), when dealing with Wooded Island, makes the following reference, presumably to this species: "Nudibranchs and Tectibranchs (*Aplysia* sp.) were extremely common. We could have obtained hundreds of specimens of *Aplysia* by merely picking them up as we waded in the shallow water."

Smith (70, p. 89) described a form *Aplysia denisoni* collected by H.M.S. 'Alert' in the following manner:—

"Body (in spirit) high, exhibiting a distinct pedal disc, produced posteriorly into a caudal termination. The entire surface dirty whitish, black-veined in the wrinkles (? stains only). Mantles-lobes moderately large, commencing in front some distance behind the posterior tentacles and terminating a little in advance of the cauda. Anterior tentacles large, cylindrical, with the apical slit not extending halfway down the outer side, placed a little nearer the oral tentacles than the beginning of the mantle-lobes. Eyes minute, situated near the outer anterior base of the tentacles. Shell very thin, straw-colour, 30 mm. long and 27 broad. Animal about three inches in length in its contracted state."

This description, while not very exact, applies closely to the present specimens. It was, however, of an animal obtained from Port Denison, Queensland, and I should have hesitated to regard it as identical had it not been possible to examine the original type-specimen in the British Museum. Smith's specimen, much discoloured by age and not well preserved, and the shell, dried and somewhat shrivelled, are still available. Taking into account the difference in condition of the specimens, I can see no way of distinguishing between them, and so I have placed the present forms under Smith's name, although they come from fairly widely-separated areas.

Genus *DOLABRIFERA* Gray, Proc. Zool. Soc. London, p. 162 (1847).

Type by tautonymy and designation:

*D. dolabrifera* Rang, Hist. Nat. Aplys. p. 51, pl. 4. figs. 1-6, ex Cuvier, Règ. Anim. (edit. i.) ii. p. 398, "1817" for 1816 (name only).

Synonymy: *DOLABRIFER* Fischer, Man. Conchyl. 1883, p. 568.

The general form is ovate-oblong or sack-like, tapering towards the tail. Tentacles and rhinophores are slit and expanded distally, the latter lie nearer to the front margin than to the dorsal slit. The eyes are as in *Tethys*. The pleuropodial lobes arise far behind the middle of the length, are contiguous, scarcely mobile, united behind, and enclose a large gill-cavity; the dorsal slit is short. The mantle is small, not perforated over the shell, nor covering much of the gill. The foot is broad, often expanded at the edges. The genital pore lies in front of the gill, under the mantle-edge. The shell is small, not spiral, solid and calcareous, and sub-triangular, trapezoidal or irregularly oblong; the apex is projecting and calloused, with no spiral tendency. The radula bears large sub-triangular rachidial teeth, with several denticles on the cusp, and the lateral teeth possess long, coarsely denticulate cusps.

Species *DOLABRIFERA PELSARTENSIS*, sp. nov. (Pl. 27. fig. 3; Pl. 29. figs. 26-28.)

*Body.* The body is oblong-ovate, reaching its maximum width behind the middle and passing backwards to a bluntly pointed tail. The back is arched and the whole integument is wrinkled, and bears a series of wart-like pointed projections. The pleuropodial lobes take their origin towards the middle region of the body; they are not easily movable, and are separated by a slit lying slightly to the right of the mid-dorsal line and mainly in the posterior half of the animal's length. At the anterior end the lobes are practically contiguous, but separated by the narrow genital groove. Within the gill-cavity, the mantle entirely covers the shell and is not perforated; it only covers a small part of the gill.

*Colour.* The colour of the preserved specimens is of a uniform dirty brownish grey, and Professor Dakin informs me that the living animals were much the same colour, but of a deeper warmer brown.

*Dimensions.* The larger specimen measured 32 mm. long by 9 mm. wide, and 8.5 mm. high.

*Head.* The head is relatively small and the front of it is occupied by the vertical slit-like mouth. It is separated from the front end of the foot by a groove. Antero-laterally it bears two split auriculate oral tentacles. The tiny eyes lie just in front of and outside the rhinophores. In the larger of the two specimens the head is practically withdrawn into the body.

*Foot.* The muscular foot is well developed and broad. At the anterior end it is bluntly rounded and, as noted, separated from the head by a transverse groove. Posteriorly it narrows off and terminates in a blunt point.

*Rhinophores.* The two rhinophores lie fairly close together, dorsally, just behind the oral tentacles and nearer to them than to the slit between the pleuropodia. Their extremities are grooved postero-laterally, but they are not so dilated as in some members of the genus.

*Gill or Ctenidium.* The gill is composed of a single lamellated plume with the lamellæ lying longitudinally, and it runs more or less transversely across the animal.

*Shell.* The shell was very small, calcareous, and apparently trapezoidal, but was too crushed to allow of accurate description.

*Labial Armature.* The labial armature, if present at all, is only very feebly developed.

*Radula.* The radula is not large, but the teeth are well developed. The total number of rows is 31. The first row consisted of 2 (*i. e.*, 1.1.0), the fifth row of 27 (*i. e.*, 13.1.13), and the twenty-fourth of 57 (*i. e.*, 28.1.28). The rachidial tooth has a broad trapezoidal basal plate, which is incurved on both its anterior and posterior edges. The blade consists of a median spine bearing two tiny laterals, and four smaller but almost equally developed spines lie on each side of this. The basal plate of the inner pleurals is rhomboidal with incurving long sides, and the blade consists of four large spines of which that nearest the rachis is usually the largest. Further out the spines become extremely large, and the one nearest the rachis much the largest, so that the others are borne on its outer side. The outermost pleurals still have a large inner spine, but the next one to it is almost as well developed, and so they appear bifid.

In general, the teeth are somewhat similar in type to those of *Tethys*, but they differ sufficiently to be recognised as of a different genus.

The genital aperture lies under the mantle-edge well in front of the gill. The seminal groove passes forwards to the penis, which is situated just below the right cephalic tentacle.

The anus opens on the right side of the middle line behind the gill.

*Notes.* The two specimens in the collection were both collected on Pelsart Island.

They do not appear to be referable to any previously described forms, and so have been recorded here as a new species with the name *Dolabrifera pelsurtensis* from the island on which they were taken.

### (3) TECTIBRANCHIATA NOTASPIDEA Fischer, 1884.

The mantle is well developed and covers the whole dorsal surface. It contains a somewhat small concave lamellar shell within a large pallial cavity. The shell may be absent or may itself be hidden by an external shell. The oral veil is marked and carries two dorsal tentacles (rhinophores). The gills are pinnate and situated laterally on the right side of the body.

## Family PLEUROBRANCHIDÆ.

The Pleurobranchidæ have not the large head-sheath of the Bullidæ nor the large parapodia of the Tethyidæ. They have a well-developed oral veil on a head marked off from the body. The oral tentacles are only moderately developed and cleft; the rhinophores are usually considerably larger and are deeply cleft longitudinally. The back is covered with a thick or a thin mantle and this generally projects freely over the head anteriorly and over the tail posteriorly. Within the mantle is a more or less large shell (absent, however, in *Pleurobranchæa* and *Oscaniopsis*). A single (in *Oscanius* double) genital aperture lies at the front end of the right side of the body. Above or below this, but still anterior to the gill, is a prebranchial opening or papilla leading into a sac. The gill is frequently tripinnate, and below it lies the urinary aperture. At the hinder end of the strand of tissue attaching the gill (the gill mesentery) lies the anus (in *Pleurobranchæa* it is above the strand). The foot is moderately large and overhung by the mantle (save in *Pleurobranchæa*, where it passes over into the side and back of the body). The sole of the tail-region of the foot often bears a gland.

Genus BERTHELLA Blainville, Man. de Mal. et Conch. 1825, p. 469.

Type by monotypy : *B. porosa* Blainville, *ibid.* = (*Bulla*) *plumula* Montagu, Testacea Brit. i. 1803, p. 214, pl. 15. fig. 9.

Type, therefore, *B. plumula* (Mont.).

Synonymy: *CLEANTHUS* Leach, Synop. Moll. Gt. Brit. 1852, p. 28.

[PLEUROBRANCHUS (*purs*) Bergh, Malak. Untern. 1808, p. 117.

The shell is haliotidiform, fairly tough, and shows lines of growth and also longitudinal striæ which, while faint, are nevertheless clearly visible. It is of a translucent amber-yellow colour.

The animal is plump and oblong; the mantle covers the whole body, its margin is entire, its front and hinder ends rounded, and it is separated from the foot by a deep groove. The gill is bipinnate and of moderate size. The two dorsal tentacles or rhinophores are inserted side by side between the mantle and the oral veil, and are auriform and deeply cleft. The foot is truncated anteriorly and bluntly rounded posteriorly where it projects slightly beyond the mantle. The labial armature is composed of two plates, each built up of a large number of irregularly arranged close-fitting spine-like pieces of chitin. The radula is well developed, without a rachidial tooth and the numerous pleural teeth have the form of knife-like blades bearing denticles at their distal extremities.

Species BERTHELLA PLUMULA (Montagu), Test. Brit. i. 1803, p. 214. (Pl. 29. figs. 29 & 30.)

*Body.* The body is an elongated oval and slightly flattened. The mantle is well developed and overhangs the body all round, save for a narrow strip at the hinder end. The oral veil also projects in front of the mantle.

*Colour.* The colour of the preserved specimen is a translucent yellow-grey, and Professor Dakin informs me that, in life, it was of a uniform dull yellow colour.

*Dimensions.* The preserved example measured 22 mm. long by 14 wide and 9 mm. high.

*Head.* The head is flattened and covered by the forward extension of the mantle. It bears a strongly developed oral veil, and this is continued out laterally into two short triangular expansions, which represent the oral tentacles and are deeply cleft along their lower outer edge. The mouth is a round opening under the head, and between it and the anterior extension of the foot.

*Foot.* The foot is well developed, and, although fairly broad, it is overhung along the sides of the mantle, but probably the posterior end is free during locomotion. The anterior end is abruptly rounded and carried on beyond the mouth as a shallow flange, and the posterior end is bluntly pointed.

*Rhinophores.* The rhinophores are well-developed cylindrico-conical structures lying under the front end of the mantle at the hinder dorsal region of the head. They arise practically touching one another in the middle line, but diverge slightly as they pass forwards and they are deeply sulcate on their outer margins. Just behind the base of each a well-marked, dull black eye-spot shows through the skin of the neck.

*Gill.* The gill is situated well forward on the right side of the body under the mantle. It is attached at the front or basal end and passes backwards as an elongated pyramidal structure, bearing about 24 lamellæ on each side of a smooth rachis.

*Shell.* The shell was, unfortunately, too damaged to admit of accurate description, but it appears to be very similar to that of *Berthella* [*Pleurobranchus*] *plumula* as described and figured by various authors.

*Labial Armature.* The labial armature consists of two oblong plates measuring 3 mm. long by 1.5 mm. wide. They are of a horn-brown colour and are composed of tooth-like elements. Each consists of a lanceolate flattened blade coming to a single, sharp, non-denticulate point, and bears, some way down on each side, a blunt triangular process, but these two projections are not opposite to one another. The elements agree with those figured by Bergh (27) and Vayssi re (75).

*Radula.* When flattened on a slide the pale yellow radula measured 4 mm. by 2 mm. It has no rachidial teeth and the pleural teeth are arranged in 78-82 rows; a typical row contains 280-290 teeth and the formula is (140-145).0.(140-145). The teeth increase in size from the rachis outwards, reaching their maximum well beyond the middle line; they then decrease slightly, but the outermost teeth, although slender, are still longer than the innermost. All the teeth are of very similar shape and stand practically upright. They have a small base, from which comes off a long

thin curved spine like the blade of a knife. At its distal extremity it bears a set of saw-like denticulations on one side, over about one-third or one-half its length. These vary in number from tooth to tooth from 7-14 and are of different sizes on the same tooth.

The genital and prebranchial apertures lie immediately in front of and below the insertion of the gill. The anus is situated just at the hinder end of the gill-mesentery.

*Notes.* This species is represented in the collection by a single specimen from Sandy Island.

Cheesman (30) has described a form, *Pleurobranchus* (perhaps *Berthella*) *ornatus*, from New Zealand, but it differs from the animal here described in having brownish mottlings on the back and dark brown rhinophores. Unfortunately, details of the radula and labial armature are not given.

According to Bergh (27) the radula of *B. [Pleurobranchus] plumula* has 100 rows of teeth 150 in a row, or, again (26), the radula is stated to contain 120 rows with about 220 in the row, but it is not clear whether the 150 and 220 in these descriptions refer to the number of pleural teeth on one side of the radula or on both. Vayssi re (75), however, while he does not state the number of rows in the radula, gives the formula as 140-155. 155-140, which agrees quite closely with that of the present specimen. The form of the teeth also falls within the limits of the variations figured by different authors for this species. The radula, therefore, appears to be somewhat variable in constitution.

The labial armature, as a whole and in its individual elements, and also the shell, as noted above, agree with previous descriptions. It would appear, then, that the present specimen belongs to the species *B. plumula*, although, if the agreement were not so close, I should hesitate to refer it to that species on account of its locality. *B. plumula*, however, had previously been recorded from Norway, Great Britain, France, Portugal, the Azores, the Mediterranean, and Lower California, so that it is of wide distribution.

#### Sub-order ASCOGLOSSA Bergh, 1876.

(Saccoglossa von Jhering, 1876 ; Elysionomorpha Pelseneer.)

Branchi e or gills are absent or poorly developed. No shell is present. The pharynx is mainly adapted for sucking and does not possess jaws. The radula is short, uniseriate, and has teeth of a characteristic shape, which, when no longer required, are passed down into a sac or ascus lying at the base of the pharynx. The central nervous system is composed of 6 or 7 ganglia massed around the  sophagus. The otocysts contain only a single otolith. Two seminal vesicles are usually present. The penis is often armed with a spine.

## Family PLACOBANCHIDÆ.

The head is flattened, and passes over laterally into short leaf- or ear-shaped tentacles, which have their lateral margins rolled. The two closely set eyes show through the skin of the neck. The body is much flattened and its sides or mantle-folds expanded into wing-like flaps (these are not epipodial developments as in *Tethys*), which are usually held up over the body. Behind the neck is a noticeable swelling, the pericardial swelling containing the pericardial cavity and the kidney, and at the right side of this lies the anus. The dorsal surface of both body and lateral expansions generally bears a series of low longitudinal folds or lamellæ. The foot is not sharply marked off from the body, its edge projects very slightly, and often its anterior end is bilabiate.

There are no jaws; the radula is short, uniseriate, and has large teeth. These, when worn, are shed into the inferior radula-sac. The stomach is short and sac-shaped. The hermaphrodite gland is not discrete, but in the form of isolated follicles. The penis is protrusible and armed with a curved spine.

Genus PLACOBANCHUS van Hasselt, *Alg. Konst en Letter-Bode*,  
1824, I. Deel, no. 3, p. 34.

Type by monotypy, *P. ocellatus* v. Hass.

The head is flattened, with a broad front, which bears on each side a short leaf-like or auriform tentacle whose side-margin is rolled. Two eyes, set close together, lie on the neck. The body is much depressed and bears two wing-like lateral expansions; these are mantle-lobes belonging to the body and not epipodial appendages as in *Tethys*; they are usually turned up over the body. Behind the neck is a fairly large pericardial swelling, on the right side of which lies the anal aperture. The upper surface of the body and the mantle-lobes bear numerous, longitudinal, parallel, low folds. The double genital aperture lies behind the right tentacle. The foot is not distinctly marked off from the body, anteriorly it is divided by a transverse groove into two equi-sized lips.

The bulbus pharyngeus is much as in Phyllobranchia. The radula is short and uniseriate, the teeth are large and persistent and passed on into an inferior sac. The penis is armed with curved spines.

Species PLACOBANCHUS EXPANSA, sp. nov. (Pl. 27. fig. 4; Pl. 29. figs. 31-34.)

*Body.* The body of this form is extremely flat and somewhat elongated. It passes out without a sharp line of demarcation into the enormously developed mantle-lobes which project, as leaf-like expansions, many times the width of the body and are continuous behind with the posterior end of the body. The whole animal presents the appearance of a flat leaf slightly thickened in the



middle anterior region. It is usual in this genus for the mantle-folds to be folded over the dorsum, but there was no suggestion of this in the present species. Indeed, these lobes are much more developed than in other members of the genus and if folded would far more than overlap. Also their antero-lateral corner projects well in front of the head, so giving the animal a characteristic appearance not found in other members of the genus.

*Colour.* The colour of the preserved specimen is a light brownish fawn with a large number of tiny black spots scattered irregularly all over it, and the mantle-margin is bordered all round with a black line about 1 mm. wide. Professor Dakin informs me that in life the colour was more of a greenish fawn with the black markings as in the preserved specimen.

*Dimensions.* The length along the middle line was 23 mm., but the antero-median corners of the mantle projected about 1.5 mm. in front of this. Width across the widest point was 21.5 mm.

*Head.* The head is flattened and abruptly rounded at the anterior end. On each side is a flattened auriculate tentacle rolled at the lateral margin. In the specimen the head was somewhat retracted.

*Foot.* The foot is practically indistinguishable, being represented simply by the thickening in the antero-median line on the ventral side. It is so reduced that it suggests that the animal was incapable of creeping.

*Branchiae.* None.

*Radula.* The radula is short and uniseriate; it contains 12-14 teeth. The tooth has an oblong base with rounded corners, and the upper portion is carried on as a long, stout, slightly curved, non-denticulate, almost conical spine. The bases of the teeth are closely approximated, so that each spine overlaps the whole of the base of the tooth immediately in front of it, and about half the next also. The spines lie down upon the succeeding tooth, which is slightly hollowed to receive them, save in the front tooth, which is almost upright and appears to be the only one in use.

The dental sac contained twenty or more discarded teeth. Some of these are quite small, not a quarter of the length of that in use, so that it would appear that they are carried for a relatively long period of time.

*Notes.* But one specimen is represented in the collection, obtained from the shore of Wooded Island.

While it is here referred to the genus *Placobranchus*, it is, as noted above, different from the previously described members of the genus in the following points:—

(1) It has non-denticulate teeth. (2) It has a relatively much greater extension of the mantle-lobes. (3) It has forward extensions of these lobes. Rather than make a new genus, however, it is included here, since in other points it agrees closely with the previously known members.

The large expansions of the mantle and almost total lack of a foot rather suggest that it may be a swimming form. The name *P. expansa* is here suggested to call attention to the large mantle-lobes.

## Sub-order NUDIBRANCHIATA Cuvier, 1817.

Nudibranchs are marine hermaphrodite Opisthobranchiata without ctenidium and osphradium, and in the adult state without a shell. The larva, however, has a shell and operculum. The visceral mass is not marked off from the foot; the body shows complete or approximate external symmetry and usually bears plumes or other appendages which assist respiration. The nervous system is concentrated in a collar behind the buccal bulb, and the chief ganglia are placed on the dorsal surface of the oesophagus, being often partially united and sometimes fused into a single mass. The vas deferens is always an internal tube, never an external groove. The teeth, when used, are discharged from the body and not retained in a sac. Among the common, but not universal, characteristics of the Nudibranchiata are also the following:—(1) The dorsal tentacles or rhinophores are often laminated and retractile, features not recorded in any other group. (2) The kidney is rarely compact, but usually a system of ramified tubes. (3) The genitalia are often extremely complicated, both in their essential plan and also owing to the presence of accessory glands and armatures. Besides this, the various subdivisions show remarkable peculiarities of their own, such as the ramification of the digestive organs, the reduction of the teeth to a single row, and the presence of nematocysts.

The classification of the Nudibranchiata here adopted is essentially that of Eliot (40) with the following four main differences:—(1) The *Aescoglossa* have been removed and treated separately for reasons noted in the introduction. Eliot's family-names *Dorididae*, *Cryptobranchiata*, and *Dorididae*, *Phanerobranchiata*, being binomial, cannot strictly be used, as the family must have a single name derived from that of its oldest and typical genus. Moreover, both these terms include a number of groups of forms, which, for the present at any rate, would appear to be more conveniently handled separately. It must be confessed that the classification of both these assemblages stands in need of further revision, a task outside the scope of the present work. (2) For the reasons just given the group *Dorididae*, *Cryptobranchiata* has been sub-divided into smaller families, whose limits correspond with the similarly named sub-families as given by Bergh in his 'System der Nudibranchiaten Gastropoden' in 1892. In certain cases the laws of priority have necessitated a change of name. (3) Eliot's four divisions of the *Dorididae*, *Phanerobranchiata* have been regarded as independent families. (4) Investigation of the synonyms of various species has revealed the fact that certain names are incorrectly applied, as was pointed out previously. These have been rectified by the alteration of the names in the cases that appear to admit of no doubt, and such a change sometimes involves both the names of the genus and the family, even though the limits of these groups have not been altered.

The sub-order is divided into two Tribes (A. *Holohepatica* and B. *Cladohepatica*), a separation dependent in the main, as the terms imply, upon

whether the liver remains in one compact mass or is split up and branched. The two groups defined in this way, however, are separated by other associated anatomical differences, that indicate clearly a wider gap between them than is perhaps suggested by the mere condition of the liver.

### Tribe A. *Holohepatica*.

Nudibranchs in which the liver forms a compact mass, neither branched nor divided, and usually accompanied by the following characters. There is complete external symmetry; the vent usually lies in the mid-dorsal line and is surrounded by a circle of branchial plumes; the radula is of moderate or considerable width, save in the family Dendrodoridæ (Doriopsidæ); mandibles are rare; the hermaphrodite gland is usually spread over the liver as a layer, but sometimes forms a discrete mass; as a rule, the genital ducts are triaulic and there are two receptacula seminis.

### Family DUVAUCELIIDÆ (TRITONIIDÆ).

The branchiæ consist of tufts set along the mantle-region or occasionally they may be absent altogether.

Genus SPHÆROSTOMA Macgill. Hist. Moll. Anim. Aberdeen, etc. (1843).

Type by monotypy: *S. jamesonii* Macgill. = *T. hombergii* Cuvier, 1803.

Type: *S. hombergii* (Cuvier).

Synonymy: TRITONIA Cuvier, Tabl. Elém. Hist. Nat. 1798, p. 387, *anct.*

NECROMANTES Gistel, Natur. des Tierr. f. Schulen, 1848, p. xi.

LEBIOPE Gistel, " " " 1846, p. 171.

The body is limaciform, but somewhat rectangular in outline, except at the end, where it tapers to a short tail. The foot is broad. Over the mouth is an oral veil bearing two grooved tentacles at the ends, and in the middle tubercles or processes. The rhinophores are retractile into raised sheaths; they are not perfoliate, but surrounded by a few plumes. The dorsal margin is slightly prominent, and bears a single row of branchial tufts which are more or less arborescent. Anal and renal openings lie on the right side. The jaws are large, with several rows of denticles or prominences near the edge. The radula varies greatly in size in the different species, but always consists of a broadish central tooth with a moderate or large number of laterals which are usually simply hamate. The first lateral is usually larger than the others, and somewhat clumsily shaped. The liver is not divided and sends off no branches to the gills. There is no armature either in the stomach or on the genitalia. The hermaphrodite gland forms a layer over the liver (*Eliot*).

It will be noted that the name of the family is changed from Tritoniidæ Cuvier, as this name is preoccupied, and Duvanceliidæ substituted. *Tritonia* Cuvier being preoccupied has to be replaced by *Sphærostoma* Macgillivray,

1843. *Duvancelia* Risso, 1826, has to replace *Candiella* Gray, 1853, as the valid name for this genus, and thus the oldest generic name in the family becomes *Duvaucelia*, from which the family-name is derived. The matter has been fully dealt with by Iredale and O'Donoghue (51 a, p. 229), and is again referred to under the Family Euphuridæ (Polyceridæ).

Species SPHÆROSTOMA DAKINI, sp. nov. (Pl. 27. fig. 5; Pl. 29. figs. 35-40.)

*Body.* The body is oblong, limaciform, and like a typical *Sphærostoma*. It is moderately high, the back flat, and there is a slight pallial extension along the edges of the back in the line of the branchial plumes. The dorsum passes forward and out as a well-marked, strongly bilobed, oral veil, which bears about six or seven dendriform processes on each side of the middle line. The short tentacle at each lateral margin of the veil is grooved throughout its length upon the ventral side.

*Colour.* In the preserved condition some of the specimens were of a dull grey colour, and some of the same general colour but plentifully marbled with dark brown. Professor Dakin informs me that the living animal is of a dirty pinkish colour with brown markings.

*Dimensions.* The specimens varied somewhat in size, and the largest measured 88 mm. long by 25 mm. wide and 25 mm. high. The lateral margins of the oral veil project about 15 mm.

*Head.* The head is sub-globose, distinct, but not projecting, and the mouth is in the form of a longitudinal cleft. It is completely overhung by the bilobed oral veil.

*Foot.* The foot is of moderate width and of the same length as the body. At the front end it is bilabiate, and posteriorly it passes back to a blunt point.

*Rhinophores.* The rhinophores are retractile within short, stout, cylindrical sheaths. This sheath is provided with a funnel-shaped collar with a wavy edge and a deep cleft on its antero-lateral side. The clavus bears a ring of six simply pinnate plumes, the most anterior is quite small, the most posterior is much larger than the others and is continued upwards as a bluntly rounded projecting cylinder.

*Branchiæ.* The branchiæ are in the form of a series of dendritic tufts along the side of the dorsum. They are paired and decrease in size as they pass backwards; the anterior plumes are attached by a wide long stalk and quite distinct from one another, but at the posterior end the stalks are shorter and closer together, so that they form a more or less continuous group. About ten large distinct plumes are present on each side, and a terminal group composed of from 3-5 smaller branchiæ. They are of the same colour as the body of the animal.

*Radula.* As in all the *Duvauceliidæ* the pharyngeal complex is very large and the radula very well developed. The total number of rows in the radula is 65-67 and the number of teeth in a row—in the first row 9 (*i. e.*,

3.1.1.1.3); in the tenth row 81 (*i. e.*, 39.1.1.1.39), and in the sixteenth row about 273 (*i. e.*, circa 135.1.1.1.135). When removed and flattened on the slide the radula measured 11 mm. along the middle line by 12 mm. at its widest point. The basal plate of the rachidial tooth is approximately rectangular, and the blade consists of three large spines, of which the median is the largest, the most pointed, and it projects well in front of the anterior margin of the basal plate. The lateral spines are blunt and much shorter. The first pleural tooth has a roughly rectangular base, but it is very irregular and it bears a single blunt and irregular spine. The remaining pleural teeth are all of a simple hamate form: they increase in size as they pass outwards, reaching their maximum between the 90th–120th, and then they decrease rapidly to the margin.

*Jaw.* The jaw, as is usual in the family, is very large and strong. Its most prominent feature is the series of serrations that mark its cutting-edge. They are quite small at the upper anterior end near the *crista connectiva*, where they first appear as the continuation of a wavy raised ridge, but they increase noticeably in size as they pass backwards. On the *processus masticatorius* they are quite large, nearly 1 mm. high and easily discernible with the naked eye. The denticles are deep brown in colour, and appear to be inserted into a lighter-coloured ridge. The well-developed jaws measure 18 mm. long by 4.5 mm. at their widest point, and are of a deep horn-brown passing off almost to black near the cutting-edge. They are somewhat narrower than in other species of the genus, and perhaps more widely divergent at their posterior ends.

The genital aperture is situated about halfway up on the right side near the level of the second branchial plume. The penis is short, conical, and unarmed.

The anal papilla lies just behind the third branchial plume, high up on the right side of the body.

*Notes.* There are five specimens of this species in the collection: three with brown mottlings and two quite grey—none with closer locality given than Abrolhos.

However, it is almost certainly the animal referred to by Professor Dakin in his report (32, p. 170) as coming from Wooded Island\*, since his remarks can apply to no other form in the collection, and the long branchiæ do give it a spurious resemblance to *Dendronotus*. He says, "Another animal which was extraordinarily abundant on this little stretch of Lagoon flat (only on the margin) was a large and beautiful nudibranch, almost certainly new and allied probably to *Dendronotus*. The singularity of its occurrence is accentuated by the fact that, notwithstanding its abundance here, not a specimen was captured anywhere else at the Abrolhos, and on our second visit in 1915 it was just as common at this place as two years before."

\* [This observation is quite correct.—W. J. D.]

of teeth in a row:—in the first row 25.0.25 (*i. e.*, 50); in the tenth row (117–120).0.(117–120), *i. e.* (284–240); and in the seventeenth row (130–135).0.(130–135), *i. e.* (260–270). There is no rachidial tooth. The inner teeth are in the form of an oblong base bearing a short curved spine. They increase noticeably in size to beyond the middle of the row, where they are hamate with a bluntly pointed corner in the middle of the back. At the outer edge they become somewhat more triangular in side-view, and the last 5–6 have a small rounded denticle near the apex of the spine.

The prominent genital aperture lies on the right side about a quarter of the length of the body from the anterior end and high up beneath the narrow mantle.

*Notes.* This species is represented by two specimens. The larger one taken from near Fremantle and the smaller from the Abrolhos Islands. The latter is interesting, because it bears the parasitic copepods described later.

The type-specimen in the British Museum described by Abraham (1) has for its locality simply Australia, it was recorded by the same author from West Australia as *C. oblongum*. Basedow and Hedley report it from Sydney Harbour, New South Wales; St. Vincent Gulf, South Australia, 20 fms.; Antechamber Bay, Kangaroo Islands, 20 fms. (?); Port Noarlunga, low water, and Salt Creek Bay, Yorke Peninsula\*.

#### Family DENDRODORIDIDÆ (DORIOPSISÆ).

The body is nearly always soft and the general shape much as in Archidorididæ. The mouth is in the form of a small pore; the tentacles are small and partly adherent; the rhinophores and branchiæ are very similar to Archidorididæ. The notæum is smooth or tuberculate; the pallial margin is well developed and often with an undulating margin. The foot is broad and much as in Archidorididæ.

The buccal tube is simple and non-glandular. The Bulbus pharyngeus is suctorial, elongated, cylindrical, and destitute of mandibles or radula. The end of the liver is deeply notched.

The penis is armed with a series of hooks.

Genus DENDRODORIS Ehrenberg, Symb. Phys. 1831

[unpaged, but on p. 94].

Type by subsequent designation: *D. lugubris* Ehrenb.; *vide* Gray,

Proc. Zool. Soc. Lond. 1847, p. 164.

Synonymy: DORIOPSIS Pease, Proc. Zool. Soc. Lond. 1860, p. 32.

Type by monotypy, *D. granulosa* Pease.

RACHODORIS Mörch, Jour. de Conch. 3rd ser. iii. 1863, p. 34.

Type by original designation, *D. laciniata* "Cuv.," *auct.*

\* [It was found later by me at Albany, King George Sound, on the South Coast of Western Australia. It has thus a wide southern range with northern extension.—W. J. DAKIN.]

fold, which is rounded at the anterior end, much wider posteriorly, and terminates in a median tongue-shaped projection. The dorsum and sides of the body are quite smooth.

*Colour.* The colour of the preserved specimen is a uniform dull yellowish brown. Basedow and Hedley (8, p. 143) give a full account of its coloration and some excellent figures (8, pl. i.), and Professor Dakin informs me that the present specimens agree with them. The general colour is shaded pinkish buff and pinkish brown; the darker colour is more prevalent towards the margin. Along the margin of the dorsum are a series of light areas, each of which has a violet-purple spot surrounded by a ring of reddish purple. The mid-dorsal region is strewn with scattered circular spots of a light violet-purple colour, in some cases surrounded by a rim of light yellow, and some of these lie in front of the rhinophores. The postero-median projection of the dorsum is covered with a network of brown lines. The sides of the body are similarly coloured to the dorsum, and have a number of small spots approximately arranged in three bands:—the upper and lower are of a rich purple and the median spots of a light violet-purple. The rhinophores and the branchiæ are of a rich reddish-orange colour.

*Dimensions.* The larger specimen, preserved in spirit, measured: 92 mm. along the foot from the tip of the tail to the front end; breadth of the body at the widest part 22 mm.; height of the body 26 mm.; breadth of the dorsum and mantle at the anterior end 22 mm.; at the posterior end 36 mm.; length of tail on dorsal side from the end of dorsum to tip 38 mm. Basedow and Hedley's measurements are "length 111, breadth 25, height 31 mm.," so that, allowing for shrinkage, the present specimen was almost the same size.

*Head.* The head is small and inconspicuous, and is completely overhung by the anterior end of the mantle. The mouth is small and in the form of a longitudinal slit running vertically. On each side of the mouth is a short sub-conical oral tentacle, which can be retracted into a sort of shallow pit.

*Foot.* The foot is linear, rounded at the anterior end, passes off to a blunt point posteriorly, and its margin is wavy.

*Rhinophores.* The club-shaped rhinophores are perfoliate, and the clavus, which is a little more than half the total length, bears a number of closely packed leaves. Each is completely retractile within a cavity, which has the margin of its aperture slightly elevated.

*Branchiæ.* The branchial plumes are twelve in number and incompletely surround the anal cone. The bases of the plumes show a marked tendency to fusion, and the posterior five on each side almost appear to arise from one ridge. Each plume is somewhat dendritic in arrangement.

They are all retractile together with the anus within a cavity that has the margin produced into a short tube.

*Radula.* The radula is strong and when removed and flattened measured 12 mm. by 9.5 mm. The number of rows of teeth is 74–76 and the number

have been wholly brown." This agrees closely with my own observations, and the peeling of the epidermis is also similar. The radula formula is given as 60.0.60, and the total number of rows 23; this is not quite the same, but the teeth are apparently identical. He says, further, "oral tentacles white; large, flat, and distinctly grooved." This is not at all in agreement with the present specimens, and, indeed, is not found in other members of the genus. Eliot's form from its teeth and other features undoubtedly is referable to this genus, and I am inclined to think that this description of the tentacles is not quite accurate.

In spite of this one serious discrepancy, the present forms agree so closely with the description of *A. affinis* given by Eliot, that I think it safer to refer them to that species than give them a new specific name.

Genus CERATOSOMA Adams & Reeve, Voyage of 'Samarang,' 1848, p. 67.

Type by monotypy: *C. cornigerium*, Adams & Reeve, *idem*, p. 68.

Species CERATOSOMA BREVICAUDATUM Abraham, Ann. & Mag. Nat. Hist. (4) xviii. p. 142, pl. 8, fig. 6 (1876). (Pl. 28, fig. 14; Pl. 30, figs. 57-59.)

Synonym: *C. oblongum* Abraham, *l.c.* p. 143, pl. 7, figs. 7, 7a, 7b.

Bergh (25) suggests that *C. caledonicum* Fischer, *C. tenue* Abraham, and *C. oblongum* Abraham are all synonyms of *C. brevicaudatum* Abraham. Basedow and Hedley (8, p. 154) call attention to the following:—in the case of *C. caledonicum*, Fischer's description indicates an animal with the lobes of the notæum more developed, and the colour-scheme in the two forms is entirely different. This being so, it seems undesirable to merge the two into one species without further evidence. The same two authors suggest that the differences between *C. brevicaudatum* and *C. oblongum* are due to the amount of contraction undergone upon or before preservation, and state that they have obtained examples of this species exhibiting similar differences from the same dredging. An examination of the external characters of the original specimens described by Abraham, and preserved in the British Museum, leads me to think that they are probably right, and that *C. oblongum* is to be regarded as synonym of *C. brevicaudatum*. I have also examined the original example of *C. tenue* described by Abraham, and, while it is possible that it may also be a synonym, it is somewhat different in appearance, and it is probably better—for the present, at any rate—to keep it separate, as has been done by Basedow and Hedley.

The specimens here described agree closely with the original description given by Abraham and that furnished by Basedow and Hedley, and are undoubtedly referable to *C. brevicaudatum*.

*Body.* The body is large, elongated, slightly wider in the middle than at the two ends, and it increases in height from before backwards to the middle or just beyond. The sides are high, almost vertical, and practically parallel. The back is flattened and continued out into a narrow undulating mantle-



*Colour.* The body-colour in the preserved state is of a pale yellowish grey, in two specimens with a deeper yellowish-brown narrow line around the edge of the notæum and the foot. In places this line bears still darker dots. In a third specimen the anterior end of the sides of the body, the notæum in front of the rhinophores and behind the branchial aperture, and the dorsal region of the tail are of an umber-brown covered with dark spots. The largest specimen has this coloration still more strongly developed, and the whole of the notæum, body, and foot is of the same umber-brown covered with dark irregular spots, and the anterior region of the notæum is of a very dark brown, almost black. Professor Dakin informs me that the living animals were similarly coloured, but the brown somewhat warmer.

*Dimensions.* The largest (and darkest) specimen measured 24 mm. long by 13 mm. wide and 12 mm. high, but this is somewhat distorted. Three others were more or less of a size, and measured 20 mm. long by 9.5 mm. wide and 9 mm. high.

*Head.* The head is small and inconspicuous; it bears a short sub-cylindrical tentacle on each side, between which the mouth appears as a small circular aperture. Each tentacle bears a longitudinal groove on its under surface.

*Foot.* The foot is moderately broad and its sides fairly parallel. The front end is abruptly rounded and the hinder end passes off to a point.

*Rhinophores.* The rhinophores have a short cylindrical stalk and sub-conical perfoliate clavus. They are completely retractile within cavities, whose rims are raised into short dark-coloured tubes.

*Branchiæ.* The five small, dark-coloured, tripinnate, branchial plumes are arranged in almost a complete and very narrow circle. They are retractile within a cavity with a circular non-raised aperture.

*Radula.* The radula when removed and flattened measured 3.5 by 2.5 mm. It is well developed and has no rachidial tooth. The number of rows is from 27-28, and the number of teeth in a row is:—in the first row 6.0.6 (*i. e.*, 12); in the tenth row 42.0.42 (*i. e.*, 84); and in the twentieth row 46.0.46 (*i. e.*, 92). The inner teeth are small simple hooks, somewhat angular and without denticles. They increase markedly in size and become simple curved hooks. Towards the outside they decrease noticeably, and they turn into short hooks only slightly curved.

The anus lies within the circle of gills at its hinder side.

The genital aperture lies about halfway up on the side near the anterior end of the body.

*Notes.* This species was represented by four specimens collected on "Wooded Island."

Eliot (38, p. 343) described a form from New Zealand of which he says, "Colour dirty white with irregular mottlings of dark reddish brown. The epidermis peels off very readily, and it is possible that the brown mottlings may have been much more extensive, or even that the dorsal surface may

*Radula.* When removed and flattened the radula measured 5 mm. by 3.25 mm. and was large and well developed for the size of the animal. The total number of rows in the radula was 83-85, and the number of teeth in each row:—in the first row 20.0.20 (*i.e.*, 40); in the tenth row 72.0.72 (*i.e.*, 144); and in the eightieth row 76.0.76 (*i.e.*, 152). There is no rachidial tooth. The innermost teeth are small but stout, and consist of an elongated base with a marked hook, on the side of which are a series of from 4-6 small triangular denticles. The teeth increase in size as they pass outwards and the hook becomes larger, bearing on its inner curved edge a series of 6-8 denticles and terminating in a rounded point. The outermost teeth are slightly smaller than those nearer the middle of the row. They have their bases much smaller, and the denticles are reduced to one or two blunt projections near the end.

The genital aperture is placed high up on the anterior end of the right side of the body.

*Notes.* In all there were six specimens in the collection: three were from the Abrolhos Islands with no further details; two were from the shore of Wooded Isle, one of which had the pharynx exerted; one was from the shore of Long Island, and this was very dark in colour.

It does not appear to correspond with any previously described form.

Genus APHELODORIS Bergh, Malakozool. Blätt. 1879, p. 107.

Type by monotypy: *A. antillensis* Bergh, *ibid.* p. 108.

In outward appearance these forms very closely resemble the *Glossodorids*, and have a well-developed notæum beyond which the tail projects. The mantle-edge only projects a very short way. The foot is fairly small, rounded in front, and not very sharply marked off from the body. The rhinophores as in *Glossodoris*. The oral tentacles are short and stunted, and have a cleft on their underside. The retractile gills are composed of a few (5) tripinnate plumes. The lips are only covered with a moderately thick cuticula. There is no rachidial tooth, and the pleural teeth are numerous and hamate. Only a posterior blood-gland is present. The prostate is large and the penis unarmed.

Species APHELODORIS AFFINIS Eliot, Proc. Malac. Soc. Lond. 1907, p. 343.

(Pl. 27. fig. 10; Pl. 30. figs. 54-56.)

*Body.* The shape of the body is typical of the *Glossodorids*. The notæum is a moderately long oval with its long sides approximately parallel and the ends equally rounded. It is carried over all round into a narrow pallial ridge. The body is fairly stout and its sides almost upright, running down to a moderately wide foot. The lower part of the body extends out beyond the notæum as a tail.

so that on the outside it obliterates the blue band and on the inside it passes across to the other side as a broad band, thus isolating, as it were, two islands of the light blue ground-colour on the notæum. Two similar bands of dark colour pass back on the dorsal surface of the tail.

In the preserved specimens all trace of the orange, red, and bright blue colours has disappeared and the whole ground-colour is of a dirty brownish fawn; the dark lines, on the other hand, are quite clearly visible. In addition to those already noted on the drawing, a narrow dark band passes around the sides of the body at the line of junction of the mantle-fold, and near the anterior end it loops downwards and backwards. It then passes back parallel with its former course, but lower down the side of the body, as a fairly broad streak running out on the dorsal surface of the tail as the two lines already noted. Under the posterior end of the mantle all these dark lines may unite and pass back right to the end of the tail as a single broad band. A narrow dark band runs right around the upper margin of the foot and out to the tip of the tail, where it may or may not unite with the lines already described.

The striking and characteristic distribution of these dark lines is fairly constant in all the specimens and shows well after preservation.

*Dimensions.* The specimens were all about the same size, and measured when preserved:—notæum 20 mm. long by 10 mm. wide; foot 22 mm. long; body 17.5 mm. wide.

*Head.* The head is quite small and overhung by the forward extension of the mantle. The mouth is a small longitudinal slit, and on each side there is a small cylindrical tentacle, much contracted in all specimens.

*Foot.* The foot is linear and its sides almost parallel. It is rounded and bilabiate in front and passes off to a pointed tail posteriorly. The sides of the foot are marked off from the body by a marginal flange. Judging from the sketch of the living animal, the tail may project beyond the notæum about half the length of the latter, but in the preserved specimens it is usually curled up and hardly projects at all.

*Rhinophores.* The rhinophores have a short stalk and a cylindrico-conical perfoliate clavus. They are completely retractile within cavities which have a slightly raised margin.

*Branchiæ.* The branchiæ are fairly simple and arranged in an almost complete circle. The anterior ones are simply pinnate thread-like plumes, sometimes tending to be bifid at the distal extremity; these number nine, although there is a tendency to fusion at their bases. At the posterior end on each side is a group of four similar, but smaller, plumes more closely united at the base, and these when extended may appear as four branches from one stalk.

The anus lies in the middle of the branchial circle. All can be completely retracted within a pocket with a circular aperture surrounded by a slightly raised margin.

genus of its own, often but incorrectly termed *Cassella* H. & A. Adams, 1858 (3).

The *Goniodoris* of Forbes, 1840 (42), still remains as a valid genus, and so does not enter the synonymy, although certain forms originally included in it really belong to *Glossodoris*.

The body is elongated and rectangular or almost square in transverse section. The smooth dorsum is an elongated oval, rounded in front and behind, and with its long sides approximately parallel. The mantle projects slightly all round and usually forms a frontal and caudal veil. The foot is large and continued backwards as a fairly long pointed tail. The sides of the body are vertical. The oral tentacles are small and conical; the retractile rhinophores have a perfoliated clavus. The retractile branchiæ are composed of simply pinnate leaves. The armature of the labial disc is strong and composed of a number of densely-set small hooks bifid at the tip. The radula contains no rachidial teeth, but there are frequently thickenings which take their place. The lateral teeth are numerous and hook-shaped; the first lateral tooth is denticulate on both sides, the rest denticulate only upon the external margin; the outward teeth are smaller, and denticulate at the extremity. The penis is unarmed.

*Glossodoris* resembles fairly closely in general appearance and shape *Goniodoris*, but the latter is phanerobranchiate. It is also much like *Aphelodoris*, but differs in the presence of labial armature, of denticulate teeth, and simply pinnate branchiæ.

Species *GLOSSODORIS WESTRALIENSIS*, sp. nov. (Pl. 27. figs. 8, 9; Pl. 30. figs. 51-53.)

*Body.* A coloured sketch by Professor Dakin from the living animal shows that its general shape was that of a typical *Glossodorid*, but the preserved specimens have shrunk considerably, more particularly in the tail-region. The notæum is a fairly narrow, flat oval, equally rounded at each end and the sides almost parallel. In the preserved specimens it contracts considerably, becoming less rectangular and more arched. The sides of the body pass inwards to a moderately narrow foot and the mantle only projects a very short distance.

*Colour.* From Professor Dakin's sketch the general body-colour appears to be a bright blue. The notæum is bordered by a narrow band, yellow on the inside and orange-red right at the margin. The rhinophores are orange-red and the branchiæ red. On the notæum inside the marginal line is a narrow band of blue and then a slightly wider band of deep purple, almost black. This deep band passes round in front and lateral to the rhinophores, and may or may not enlarge slightly to include the margin of their sheaths. At the posterior end it passes round more or less parallel with the margin and behind the branchiæ. In the middle of the notæum the dark band enlarges.

Genus *Glossodoris* Ehrenberg, 1831, Symb. Phys. [unpaged, but on p. 92].

Type by subsequent designation: *G. xantholeuca* Ehrenb. Red Sea. Gray, Proc. Zool. Soc. Lond. 1847, p. 164.

But *G. xantholeuca* Ehrenb. = *Doris pallida* Rüpp. et Leuck., 1828.

The type is therefore here designated *G. pallida* (Rüpp. et Leuck.), 1828.

Synonymy: *ACTINODORIS* Ehrenberg, 1831.

Type by monotypy: *A. spmsa*, Ehrenb. Symb. Phys. [p. 93]; *vide also* Gray, Proc. Zool. Soc. Lond. 1847, p. 164.

*PTERODORIS* Ehrenberg, 1831.

Type by subsequent designation: *P. picta* Ehrenb., Gray, Proc. Zool. Soc. Lond. 1847, p. 164.

*CHROMODORIS* Alder & Hancock, 1855.

Type by original designation and monotypy: *D. magnifica* Quoy et Gaim., Alder & Hancock, Mon. Brit. Nud. Moll. pt. vii. 1855, p. xvii.

*GONIOBRANCHUS* Pease, 1866.

Type by designation: *G. vibrata* Pease, Pease, Amer. Jour. Conch. ii. 1866, p. 204.

*Chromodoris*, the generally accepted name for this genus, was introduced by Alder and Hancock (*vide supra*). These authors in a subsequent paper (6, p. 115) say:—"The *Goniodoris* of Forbes has hitherto been considered a northern form—the southern species which some authors have referred to it belonging almost without exception to the allied genus *Chromodoris*, which, on the other hand, has not been found further north than the Mediterranean." The name thus introduced was used by Bergh (11, p. 72), who gives as synonyms *Doriprismatica* d'Orbigny and *Goniobranchus* Pease, and again in 18 (p. 1), but this time with the synonyms *Glossodoris*, *Actinodoris*, and *Pterodoris*, all of Ehrenberg, 1831, twenty-four years earlier than Alder and Hancock's name. Bergh points out there and again in 1884 (23, p. 65) the identity of Ehrenberg's genera with that of Alder and Hancock, and in this he is right.

Thus, in spite of the common usage of the generic designation *Chromodoris*, there is no doubt that Ehrenberg's names have considerable priority. The question as to which name should be employed is easily settled, for, while they were all published at the same time, *Glossodoris* comes first in order, and the first species is given as *G. xantholeuca*, which Gray (44, p. 164) designated as the type-species. Bergh, in a paper where he re-examines Ehrenberg's types, states, in our opinion rightly, that *G. xantholeuca* is the *D. pallida* (Rüpp. et Leuck.), and that all species of *Glossodoris* are congeneric. The genus then stands as *Glossodoris* with the type-species *G. pallida* (Rüpp. et Leuck.).

In various places Bergh includes *Doriprismatica* d'Orbigny, 1837 (11), as a synonym; but, while part of d'Orbigny's genus belongs to the present group, the type, *D. atromarginata* Cuv., 1804, is in reality a member of a

The genital aperture, as usual, lies on the right side of the body near the anterior end.

*Labial Armature.* No labial armature was found.

*Notes.* One specimen only is in the collection, and this was accompanied by the locality-label "Shore of Wooded Isle."

Eliot (36, pp. 305-356) calls attention to the difficulties encountered when trying to determine the position of a Cryptobranchiate Dorid, and in dealing with the present form they have come before me frequently. Bergh's family Dorididæ (Cryptobranchiatæ) is divided into five sub-families and about 30 genera, practically all of which were created by Bergh himself, and certain of them contain only a single species. The differences between some of the genera are so slight that, unless Bergh's own species are dealt with, it is difficult to determine where to place a new form. There seems no doubt that the whole family stands in need of considerable revision before it can be regarded as satisfactory. The present specimen agrees closely with the genus *Asteronotus*, and in general form, and perhaps even colour, somewhat resembles the *A. hemprichi* Ehr. as figured by Eliot (36, pl. xxxiv.), but it differs in certain points. The radula formula is different, the individual teeth are not quite same, the branchiæ number five, etc. For these reasons I have described it as a new species under the name of *Asteronotus fuscus*.

#### Family GLOSSODORIDIDÆ (CHROMODORIDINÆ Bergh).

It has been pointed out above that Bergh's binomial family-name **Dorididæ Cryptobranchiatæ** cannot possibly be allowed to stand. It is proposed, therefore, to split this group into several families, of which one is the same as the old Chromodoridinæ of Bergh. But, as the name *Chromodoris* has to be set aside for the older name *Glossodoris*, the family-name must be changed as above.

The body is elongated, compressed, and soft; the colour is striking, often magnificent, and generally with lines or spots; the notæum is nearly always smooth, the pallial margin is fairly broad at the anterior and more particularly at the posterior end, but usually quite narrow in between; the tentacles are small, conical, and generally partly eversible; the branchial plumes are usually simply pinnate.

The labial armature is strong and composed of minute rods. The rachis of the radula is very narrow and often furnished with minute compressed pseudo-teeth; there are numerous pleural teeth of hamate form and generally with a denticulate margin, the first teeth are usually denticulate on both sides.

There is no proper ventricle.

The penis is unarmed.

The penis is unarmed, the prostate large, and, according to Bergh, a glandula and hasta amatoria are present.

Species *ASTERONOTUS FUSCUS*, sp. nov. (Pl. 28. figs. 12, 13; Pl. 30. figs. 48-50.)

*Body.* The body is shaped like a typical Dorid—oval and with a moderately arched dorsum. The mantle is well developed, and projects considerably beyond the foot all round. The whole animal is like a piece of india-rubber to feel. The dorsum bears a series of raised elongated tubercles, the largest of which forms an irregular ridge stretching from between the rhinophores back to the branchial aperture. From this median projection a number of unequal and irregular short side-ridges are given off, getting lower as they pass from the middle line, and all around the margin is a number of small oval or roundish tubercles.

*Colour.* The colour of the preserved specimen is a muddy-brown, and a note included with it states that it was "dirty brown, rough surface." Professor Dakin informs me that it was of a dirty brown with some lighter brown spots, but no conspicuous colour-pattern.

*Dimensions.* The specimen measured 27.5 mm. long by 15 mm. wide and 9 mm. high, and the foot 24 mm. by 6.5 mm.

*Head.* The head is quite small with a small mouth in the form of a short transverse slit, and on each side is a small tentacle.

*Foot.* The foot is only moderately broad, with an undulating margin. The anterior end is bluntly rounded, strongly bilabiate, the upper lip is indented in the middle line, and the posterior end is pointed.

*Rhinophores.* The rhinophore has a bluntly conical, perfoliate clavus with a fair number of thin leaves and a short cylindrical stalk. They are completely retractile within cavities, whose margins are slightly raised, so that they look somewhat like a tubercle. In the preserved specimen they are of a yellow colour.

*Branchiæ.* The branchiæ are five in number, each consisting of a large, branched, plume-like gill, arranged in a circle. They are completely retractile within a cavity with a raised margin, so that it stands up like one of the larger tubercles. The edge of this is furnished with six small lobes, which, when the aperture is tightly closed, are tucked inside.

*Radula.* The pale yellow radula when flattened on a slide measured 3 by 2.75 mm. and contained 38-40 rows of teeth. A median tooth is absent, and the number of pleurals in each row was:—in the first 6.0.6 (*i.e.*, 12) and in other rows from the third on 65.0.65 (*i.e.*, 130). The teeth themselves are simply hamate and increase in size as they pass outward to beyond the middle of the line. They decrease in size rapidly at the outer margin, and the last one or two are reduced.

The anus lies on a well-marked papilla in the middle of the branchiæ, and it bears at its base the small oval excretory pore.

*ALLOIODORIS HEDLEYI* mihi.—Colour preserved; dark muddy-fawn with a tinge of green with irregularly scattered dark brown, almost black, roughly circular, ring-shaped marks (*O'D.*). Colour alive: yellowish white to greyish brown, covered with minute spiculose elevations on the dorsal surface, which impart to it a brownish tint; also less numerous, larger elevations, surrounded by irregular circles of deep brown. The latter occasionally have a centre of opaque white surrounded by a ring of reddish brown.

No labial armature. Tentacles small, sub-cylindrical, 1.25 mm. long. Size 52 mm. long, 34 mm. wide, 23.5 mm. high. Radula 33–35 rows (55–57). 0. (55–57). Innermost pleurals small, but much like the remainder, not like those of *A. lanuginata*; outer teeth not denticulate.

I think it will be seen from the above that three distinct forms appear to be represented, of which *A. marmorata* Bergh and *A. hedleyi* mihi, while resembling one another more closely than either of them does *A. lanuginata*, are, nevertheless, distinct species. The form described by Basedow and Hedley is not the same as that recorded by Bergh, and hence it is in need of a new name. I propose to call it *A. hedleyi* after Dr. Charles Hedley, who has added so much to our knowledge of the marine fauna of Australia.

#### Family PLATYDORIDIDÆ.

The body is somewhat flattened, of leathery consistency, sometimes tough and sometimes brittle; it has an oval or sometimes almost circular outline; the notæum is fairly smooth or minutely granulate, the dorsum often marked by tubercles or ridges; the pallial margin is ample; the branchial aperture is generally stellate: the tentacles are digitate; the anterior margin of the foot is bilabiate, and the upper lip indented or split in the middle line.

There is no labial armature; the radula lacks rachidial teeth; the pleural teeth are numerous and hamate.

The prostate gland is large.

(Genus *ASTERONOTUS* Ehrenberg, 1831.

Type by monotypy: *A. hemprichii* Ehrenb. Symb. Phys. (1831).

The body-form is oval and somewhat flattened; the animal is of a peculiar leathery or india-rubber-like consistency, not hard or brittle. The skin is smooth to the touch, but covered with raised protuberances in the form of ridges, of which one well-marked one runs in the mid-dorsal line from between the rhinophores back to the branchial aperture. The margin of this aperture is produced into lobes (usually six). The foot is narrow, bilabiate anteriorly, and the upper lip indented.

There is no labial armature; the radula has no median tooth and the pleural teeth are simply hamate.



Mr. E. Ashby, who is familiar with this form on the coast of South Australia, informs me that they are usually of the smaller size. It has not been recorded previously from West Australia.

Some confusion exists in regard to the nomenclature of the members of this genus, which deserves comment.

The following forms have been recorded :—

*A. (Doris) lanuginata* Abraham, Proc. Zool. Soc. Lond. p. 255, pl. xxix. figs. 15–17 (1877).

*A. marmorata* Bergh, Malak. Unters. vi., Semper's Reisen, 1904, p. 42.

*A. marmorata* Bergh (*sic*), Basedow & Hedley, Trans. Roy. Soc. South Australia, vol. xxix. p. 152 (1905).

*A. lanuginata* Abr., Eliot, Proc. Malac. Soc. Lond. p. 333 (1907).

*A. hedleyi* mihi, described above.

The original specimen described by Abraham is in the British Museum; it is not well enough preserved for detailed examination and the pharyngeal complex is removed. Eliot (98, p. 333) states that, on comparing this specimen with that sent by Suter from New Zealand, he has no doubt that they are identical. He gives the genus as containing two species (*A. lanuginata* Abr. and *A. marmorata* Bergh), but lower down on the same page he gives *A. marmorata* as a synonym of *A. lanuginata*, and on p. 335 he states that Bergh's *A. marmorata* is perhaps a distinct species. Further, he suggests that it is not clear that the animal figured by Basedow and Hedley is either of the two species. On comparing the descriptions we find :—

**A. LANUGINATA** (Abr.).—Colour preserved “greenish-grey, blackish mottlings” (Eliot). In the specimens in the British Museum the mottlings are uniformly dark areas (*PD*). Colour in life “dirty red, numerous white pustules” (Suter), but the applicability of this to the specimen is doubtful.

A weak labial armature. Tentacles long, flat, furrowed on upper surface, and almost auriculate. Rhinophores much closer together in large specimens of *A. hedleyi* than in the far smaller original specimen of *A. lanuginata*. Size 50 mm. long, 33 mm. broad, 16 mm. high. Radula 26 rows, (40–45). 0. (40–45). 1st and 2nd teeth characteristic, unlike *A. marmorata* or *hedleyi*.

**A. MARMORATA** Bergh.—Colour preserved “von hell gelblichweisser Farbe, die von zahlreichen kleineren und (bis 3 mm. diam.) grosseren hell aschegrau, verschwimmenden, unregelmässigen Flecken unterbrochen war” (no mention of spots being ring-shaped, which would have hardly escaped Bergh's acute eye).

Labial armature not mentioned. Tentacles 1.5 mm long, “finger-formig.” Size 45 mm. long, 25 mm. broad, 13 mm. high. Radula 34–35 rows, (40–42). 0. (40–42). 1st and 2nd teeth like remainder, outer teeth denticulate and not quite same shape as *A. hedleyi*.

A similar series of markings is present on the under surface of the mantle. The foot is slightly lighter in colour and speckled with dark brownish-black spots.

*Dimensions.* The largest specimen measured 52 mm. long by 34 mm. wide and 23.5 mm. high. The foot measured 42 mm. long by 16.5 mm. wide. Thus it is larger than Bergh's specimen of *A. marmorata* (45 by 25 by 13 mm.), and considerably larger than the measurements given by Basedow and Hedley (22.5 by 10 mm.).

*Head.* The inconspicuous head is very small and tucked in between the front margin of the foot and the large overhanging mantle. The mouth appears as a tiny longitudinal slit, and the oral tentacles are sub-cylindrical and when contracted measure 1.75 mm.

*Foot.* The foot is elongated and narrow; the front end deeply bilabiate and rounded; the hinder end bluntly pointed and in the specimen not quite reaching to the edge of the mantle.

*Rhinophores.* The rhinophores are club-shaped, and the perfoliate clavus occupies almost three-quarters of their length. They are completely retractile within cavities with a circular, slightly raised aperture.

*Branchiae.* The branchiae were six in number. Basedow and Hedley (8) state that they were seven or eight, but show only six in their figure. They are retractile within a cavity which opens by a raised, transversely oval aperture with a wavy margin.

The anal papilla lies within the circle of gills; it is low and bears the renal aperture on its right anterior base.

*Radula.* The radula is well developed, and when removed and flattened measured 6 mm. along the middle line and 5.5 mm. at its widest point. The total number of rows in the radula was 33-35 and the rows contained:—the first row 6.0.6 (*i. e.*, 12) teeth; the tenth row 55.0.55 (*i. e.*, 110) teeth; and the thirtieth row 57.0.57 (*i. e.*, 114) teeth. The innermost pleural teeth are small, and consist of a curved spine on an elongated basal plate. They increase very markedly in size to beyond the middle of the row, where they are falciform, and then they decrease again towards the outside. No sign of denticles was found on the lateral teeth.

*Labial Armature.* None was noticed.

The glans penis is armed with a series of rows of hooks.

The hermaphrodite gland is discrete and does not form a layer over the liver.

*Notes.* The collection included three specimens. One small one from Pelsart Island and the other two larger ones with no definite locality-label.

The specimens described by Basedow and Hedley (8, pp. 139 and 152) are from St. Vincent's Gulf and Port River, South Australia, and from Edithburgh, York Peninsula. It has been noted that the specimens here measured are considerably larger than those measured by Basedow and Hedley.

he gave no anatomical details, so that the above is the first description of the radula etc. of the species.

#### Family ARCHIDORIDIDÆ.

The body is not hard and slightly depressed; the notæum is tuberculate or granulate, the pallial margin is fairly broad; the tentacles are small; the branchial plumes are nearly always tri- or quadripinnate; the foot is fairly broad. There is no labial armature. The radula has no rachidial tooth; the pleurals are numerous and hamate. The penis is generally unarmed.

#### Genus ALLOIODORIS Bergh, 1904.

Type by monotypy: *A. marmorata* Bergh, Malak. Unters. vi., Semp. Reis. 1904, p. 42.

The body is depressed, the notæum minutely granulose and fairly broad. The branchiæ are not numerous and generally tri- or quadripinnate. Labial armature is feeble or absent. The foot is strong and as wide as the body. The mantle is fleshy and well developed. There is no rachidial tooth. The lateral teeth are numerous and hamate. The last part of the vas deferens in the penis bears a series of hooks. The hermaphrodite gland forms a discrete mass quite distinct from the liver.

This genus was founded by Bergh on some specimens from Tasmania, and is remarkable in that the hermaphrodite gland forms a discrete mass and is not spread out as a layer over the liver. This is a condition encountered also in *Bathydoris* and *Trevclypna*, forms that for other characters are quite widely removed from the present genus. Eliot suggests (38, p. 333) that this perhaps represents an older condition than that in which the gland is spread over the liver. "and it would seem that very different families of the Dorididae sporadically preserve or revert to the older arrangement."

Up to the present only two species have been referred to the genus, viz., *A. marmorata* Bergh and *A. lanuginata* Abr.

Species ALLOIODORIS HEDLEYI, sp. nov. (Pl. 27. figs. 6 & 7; Pl. 30. figs. 45-47.)

Synonymy: *A. marmorata* Basedow & Hedley, Trans. Roy. Soc. South Austr. 1905, p. 152, non Bergh.

*Body.* The general shape of the body is elliptical, slightly broader at the posterior end, and only moderately convex. The entire dorsal surface is covered with minute spiculate papillæ, making it somewhat rough to the touch. The mantle is very well developed, being much wider than the foot, and its fairly thin edge is wavy and undulating.

*Colour.* The colour of the preserved specimen is a dark muddy-fawn with a tinge of green. Irregularly scattered over it are a series of dark brown, almost black, roughly circular, ring-shaped marks from 2-3 mm. wide,

*Head.* The head is fairly large and sub-globose; the mouth is large and conspicuous, having the form of a longitudinal slit. On each side of it is an oral tentacle in the form of a large somewhat ear-shaped flap with a wavy margin. This measured 27 by 24 mm.

*Foot.* The foot is well developed, strong, and muscular. Its front end is abruptly rounded and bilabiate, and the hinder end passes back to a blunt point. The sides of the foot are thrown out into a wide, folded, undulating flange which, in the large preserved specimen, projected 16–17 mm.

*Rhinophores.* The rhinophores are well developed, and the sub-conical perfoliate clavus with 55–60 leaves is set at an angle of about  $45^{\circ}$  to the cylindrical stalk. The stalk is surrounded by a tubular sheath with a smooth margin, and in some specimens the clavus is retractile within this.

*Branchiae.* The six branchial plumes are dendritic, very conspicuous, and arranged in a wide circle. Each of the anterior two pairs gives off a small branch from the base, but the posterior pair each arise by two equally developed main stems coming from the same point.

*Radula.* The radula is well developed and strong, and when removed and flattened measured 10.5 mm. along the middle line and 10 mm. at its widest point. The total number of rows in the radula is 47–49, and the number of teeth is in the first row 40 (*i.e.*, 20.0.20), in the tenth row 130 (*i.e.*, 65.0.65), and in the forty-fifth row 152 (*i.e.*, 76.0.76). There is no rachidial tooth. The inner pleurals consist of a roughly rhomboidal basal plate with a small curved spine at the antero-median corner. As they pass outwards they increase in size, the base gets longer, and the spine increases very markedly. They reach their maximum just beyond the middle of the row, and then decrease in size mainly in the basal plate. Thus it comes that, while the inner pleurals are mostly basal plate with a small spine, the outermost teeth are mainly spine with a small basal plate.

*Labial Armature.* The lips are guarded by a thin tough membrane which is beset with a large number of tiny hooked spines.

The anus is not conspicuous and lies within the circle of gills towards the hinder end.

The genital aperture is well marked, and situated up on the right side of the body behind the level of the front end of the foot. The penis is long and unarmed.

*Notes.* Five specimens were in the collection:—

A large one and a moderately large one with no locality-label.

Two smaller ones from Pelsart Island.

One of fair size from Wallaby Island.

These specimens were obtained from the same place as Kent obtained his *H. imperialis* and are thus topotypic with it. While he gave a coloured drawing of the living form, with which the present specimen agrees closely,

It does not appear to agree with any previously recorded species, and so is described here as new with the name *Sphaerostoma dakeni*, after my friend Professor W. J. Dakin, who collected it.

Family HEXABRANCHIDÆ.

This family contains only one genus, and its characters are those of the genus.

Genus HEXABRANCHUS Ehrenberg, Symb. Phys. (1828).

Type by monotypy: *H. prætextus* Ehrenb., pl. 1. figs. A-C.

N.B.—The plates in this work were published in 1828 and the text in 1831. This form appears on the plates.

The body is large and of an elongate-oval shape; the back is smooth and broad. It passes out laterally to a folded margin, which is continued out as the enormous sheet-like much folded mantle, which may be wider than the body. The branchial plumes, generally 6-8, are dendritic and distinct, and arranged in a circle around the anus. They are not retractile, but contractile, and their bases are surrounded by a shallow wide-open depression. The rhinophores have a cylindrical stalk and a perfoliate clavus set at an angle to it. The oral tentacles are large and auriculate with a folded margin. The foot is relatively well developed. The labial armature is well developed and composed of tiny hooked spines. The radula is well developed, with no rachidial tooth, and the pleural teeth are numerous, hamate, and have no lateral denticles. The penis is long and unarmed. Only the posterior blood-gland is present. Bergh classes these as a sub-family of the Dorididæ Cryptobranchiatæ. This name cannot stand, and the forms are not even Cryptobranchiate. They are here raised to a separate family.

Species HEXABRANCHUS IMPERIALIS Kent, Nat. in Austr. 1897, p. 150.  
(Pl. 28. fig. 11; Pl. 29. figs. 41-44.)

*Body.* The body is moderately stout, of an elongated oval shape, and the skin is smooth. The most striking feature, however, is the mantle, which is extraordinarily well developed and takes the form of a thin wide flange, wider than the body, passing all round save at the anterior end, where it is only narrow. The rhinophores with their sheaths stand up prominently at the anterior end, and the circle of gills is conspicuous at the hinder end.

*Colour.* The colour of the preserved specimens is a dull greenish grey without any indications of markings. Professor Dakin says it is identical with Saville Kent's drawing, and that at a distance it looked not unlike a great piece of fresh lung torn from a vertebrate. Kent figures it as of a flaring red colour all over with no markings.

*Dimensions.* The body of the largest specimen measured 125 mm. long by 50 mm. wide and 44 mm. high. Beyond this the mantle extended 80 mm. along each side, 45 mm. across the posterior end, and 6 mm. across the anterior end as a sort of oral veil.

*DORIOPSIS* Alder & Hancock, Trans. Zool. Soc. Lond. vol. v. pt. 3, 1864, p. 125.

Type by original designation, *D. gemmacea* Ald. & Hancock.

*HAUSTELLODORIS* Pease, Amer. Jour. Conch. vol. vi. 1871, p. 290, for the *Doridiopsis* of Alder & Hancock.

*Doriopsis*, the generally accepted name for this genus, was introduced by Pease, 1860 (62), who failed to give a satisfactory definition of the genus. Of it Bergh (11, p. 83) says: "Das Geschlecht *Doriopsis* wurde von Pease in der gewöhnlichen Art des Heeres von Art- und Geschlechte-Fabrikanten mit ganz flaschen Characteren schon in 1860 aufgestellt."

Four years later Alder and Hancock (6) more accurately described the same genus, but gave it the name *Doridopsis*, without, however, referring to Pease's genus or species. Again, the following year Hancock (46) gave a detailed description of the genus, also without reference to the work of Pease. The latter author in 1871 re-affirmed his genus, claimed that the genus of Alder and Hancock was not identical, and suggested for their genus the name *Haustellodoris*. There can be no doubt, however, that all the species of both authors belong to the same genus.

However, Ehrenberg in 1831 had founded the genus *Dendrodoris* for two species, one of which (*D. lugubris*) was subsequently designated the type by Gray (44, p. 164). Bergh (18, p. 21) points out that Ehrenberg's definition of the genus is incomplete and unsatisfactory, although both the species included within it are recognisable and without doubt belong to the genus subsequently termed *Doriopsis*. He further says (*l. c.* p. 22), "Es liegt daher um so mehr wohl kein Grund vor, die Benennung *Dendrodoris* für die durch Hancock und durch mich jetzt so gut bekannten Doriopsen zu restituieren."

This is a strange line of reasoning to follow, for, in the first place, Hancock uses the term *Doridopsis*, not *Doriopsis*, and was not the author of either name. Secondly, while admitting that both Ehrenberg's original species belong to the genus under discussion, Bergh prefers to adopt a much later term, not simply incompletely defined, but actually with "ganz flaschen Characteren."

There seems little doubt that the genus should stand *Dendrodoris* Ehrenb. with *D. lugubris* Ehrenb. as the type by subsequent designation, and so the name of the family also needs to be altered to Dendrodorididae.

It is interesting to note that the same species is described under the same name, *Doris lugubris*, by Gravenhorst (43 a) in the same year, 1831. I have been unable to ascertain whether Gravenhorst's or Ehrenberg's name has priority, but, in any case, it does not alter the generic name.

Species *DENDRODORIS NIGRA* (Stimpson), Proc. Philad. Acad. Nat. Sci. vol. vii. 1855, p. 380.

Synonymy: *Doris nigra* Stimpson, 1855.

*Doriopsis nigra* auct.

*Doridopsis nigra* auct.

*Body.* The body is of moderate size, elliptical, and somewhat depressed. The dorsal surface is finely granulate, while the mantle is more smooth. The

mantle is well developed, fairly thin, and extends beyond the body all round, save that the tip of the tail probably projects slightly during locomotion.

*Colour.* In the preserved specimens the colour is black, shading off to a dark grey near the mantle-margin, but showing no sign of the red margin described by Stimpson in the living animal. It is covered irregularly with tiny white spots, which grow more abundant and larger towards the margin of the mantle. The branchiae are of the same dark colour as the body. The under surface of the foot is also of a dark grey shade. In life the white spots are more striking and the sole of the foot of lighter grey.

*Dimensions.* The specimens varied in size, and the largest measured 23 mm. long by 15.5 mm. wide and 9.2 mm. high. The smallest was only 12.5 mm. long.

*Head.* The head is very small and inconspicuous, and bears a much reduced tentacle at each side. The mouth is a small circular pore lying between the lips of a deep cleft in the anterior margin of the foot.

*Foot.* The foot is moderately large; its sides are continued out a short distance as shallow flanges and its posterior is bluntly pointed. The front end is deeply cleft, and between its margins, as noted above, the mouth is situated.

*Rhinophores.* The rhinophores are fairly small, completely retractile within sheaths with smooth circular margins, and bear a perfoliate clavus on a short cylindrical stalk.

*Branchiae.* The tripinnate branchial plumes are eight in number and arranged in the form of a circle, incomplete behind, but the gap is filled in by the low anal papilla. They are of the same general colour as the dorsal surface.

*Radula.* No trace of a radula or pharyngeal complex is present. The oesophagus takes the form of a straight narrow tube.

*Notes.* In all seven specimens were represented in the collection: three large specimens from Sandy Isle; three smaller specimens from Wooded Isle; one deformed and swollen specimen from Pelsart Island.

This species of *Dendrodoris* seems to be widely spread in the Indian and Pacific Oceans, and the type-specimen was described from Loo Choo and Kikaisima.

Species *DENDRODORIS MAMMOSA* (Abraham), Proc. Zool. Soc. 1877, p. 266, pl. lxix. figs. 20–21. (Pl. 28. fig. 15.)

Synonymy: *Doris mammosa* Abraham.

*Doriopsis mammosa* auct.

*Doridopsis mammosa* auct.

*Body.* The body is fairly large and of an elongated oval shape. The mantle is strongly developed, and projects all round as a thin fold about half the width of the body, and has a wavy margin. The very soft dorsum and in part the mantle also are covered with very large irregular warty

protuberances, giving them a very uneven appearance. The large projections also have smaller ones near their bases, and similar small ones are scattered over the general dorsal surface. Three noticeably large projections lie on each side between the rhinophore and the gills, and two more are situated between the rhinophores.

*Colour.* The general body-colour of the preserved specimen is a dirty yellowish grey, becoming darker towards the periphery. Down the middle of the back is a series of three large roughly rhomboidal black marks, which have other very dark, almost black, markings within them. Five or six similar but slightly smaller marked areas lie lateral to the large projections on each side, the first pair of lateral marks being in front of the rhinophores and the last behind the branchiæ. The clavus of the rhinophore is light-coloured and the tips of the branchiæ very dark; Professor Dakin informs me that in life the pattern was similar, but the colours brighter and the contrast more marked.

*Dimensions.* The preserved specimen measured 72 mm. long by 40 mm. wide (mantle extended) by 17 mm. high. The foot measured 65 mm. long by 15 mm. wide, so that the mantle, when extended, projected 12.5 mm. beyond the foot.

*Head.* The head is extremely small and inconspicuous, and the mouth is a tiny aperture lying between the two edges of the front end of the foot. On each side of the head is a tiny flap-like tentacle about 1.5 mm. long, partly retracted within a shallow groove-like cavity.

*Foot.* The foot is well developed, long, fairly narrow, and with an expanded flange-like margin. At the anterior end the foot bears a deep longitudinal cleft, between the edges of which lies the mouth.

*Rhinophores.* The rhinophores are fairly small clavate structures with a perfoliate clavus, and are entirely retractile within cavities provided with an elevated tubular margin. They lie fairly close together near the anterior end.

*Branchiæ.* The five branchial plumes are tripinnate and arranged in a fairly close circle, with a tendency to fusion at their bases. Each is dendri-form. They are retractile within a wide shallow cavity with a slightly raised margin.

*Radula.* No trace of a radula or pharyngeal complex is present, and the first part of the œsophagus is in the form of a straight narrow tube.

The anus lies between the bases of the two hindmost gill-plumes upon a fairly well-developed sub-conical papilla.

The genita aperture is, as usual, high up on the right side of the body about one-quarter of the way from the anterior end.

*Notes.* Only one specimen is represented in the collection with a label "Nudibranch from Fremantle, W.A." It is not therefore an Abrolhos type, so far as we know.



The type-specimen described by Abraham (2) measured 56 mm. long by 44 mm. broad and 16 mm. high, so that it was not so large as the present one. No locality is given, but it is stated to be "obtained during the Antarctic Expedition." \*It was possibly obtained at some port of call, however, for the Dendrodorids as a genus are characteristic of the warmer seas.

Family EUPHURIDÆ (POLYMERIDÆ, POLYMERADÆ).

The body is more or less elongated and limaciform. The dorsum is not marked off from the sides or separated by a prominent margin. The frontal veil is more or less prominent, simple, or furnished with simple or compound appendages, and the dorsum generally has a solitary dorsal appendage (branchialis) or several dorsal and lateral. The branchiæ are generally paucifoliate, but may be composite; they are not retractile within a cavity. The tentacles are small, lobiform, folded, or auriform. The foot is not broad, and generally rounded anteriorly. The bulbous pharyngeus is simple. The buccal cavity is often armed with laminae (often composed of minute rods). The radula nearly always has no rachidial teeth; the majority of the pleural teeth are uncinatè, and the outermost teeth simple, not hamatè. The glans penis is armed; two spermathecas are present.

In 1798 Cuvier instituted the name *Tritonia* for a genus of Nudibranchs, but while describing the genus he mentioned no particular species, and later, in 1803, he enlarged this description and dealt with a definite and new species, *T. hombergii*. Lamarck in 1801 took Cuvier's name and gave as a species of the genus *T. clavigera*. Rafinesque in 1815 proposed the name *Euphurus* for the *Tritonia* of Lamarck—i. e., with *T. clavigera* as a type. At a later date Johnston (1838) dismissed Lamarck's species as being outside the limits of Cuvier's genus, and proposed for it the name *Triopa clavigera*, under which it has since been dealt with. To turn to other animals than Nudibranchs, however, we find that in 1774 *Tritonium* was employed as a generic name by Müller, and in 1800 Meigen used *Tritonia* as the name of a genus.

Thus it will be seen that the term *Tritonia* as applied to Nudibranchs refers to two entirely different and unrelated forms, and in any case the name is pre-occupied. As noted previously, *Tritonia* Cuvier (i. e., with *T. hombergii* as type) has to be replaced by *Sphaerostoma* Macgillivray, and as will be seen above *Tritonia* Lamarck (i. e., with *T. clavigera* as type) becomes *Euphurus* Rafinesque, and this intercepts the later name *Triopa* Johnston. In this way the oldest generic name in the present family becomes *Euphurus*, from which the family-name is derived. This matter is also referred to by Iredale (51) and Iredale and O'Donoghue (51 a).

Genus NOTODORIS Bergh, Journ. Mus. Godeffroy, viii. 1875, p. 64.

Type by monotypy: *N. citrina* Bergh, l. c.

The body is limaciform with the sides not marked off from the dorsum; it is hard and rough, often marked with prominent ridges. The frontal veil

is large. The branchiæ and sometimes the rhinophores are protected by valves. The rhinophores are not perfoliate. There is no labial armature of rods or spines, but a chitinous ring may be present. No rachidial tooth is present; the pleurals are similar and hamate with indications of an accessory denticle.

Species NOTODORIS GARDINERI Eliot, Fauna & Geog. Maldives and Laccadive, vol. ii. pt. 1, 1903, p. 548. (Pl. 28. figs. 18, 19; Pl. 30. figs. 62-64.)

*Body.* The body is limaciform and covered with small tubercles, which are more numerous and larger at the anterior end. Nearly halfway back the body reaches its highest point, and here arise the branchiæ covered by their three characteristic protecting valves. A row of larger tubercles runs from the sides of the oral veil to the branchial valves. Beyond this the body falls to a lower, narrower, tail-like region. A well-marked valve-like tubercle lies on the outside of each rhinophoral aperture, and between these openings is a group of two or three large tubercles. Lateral to the rhinophores the notæum passes out and forwards as a very well-marked oral veil with a tuberculated margin. The very tough skin contains a number of very hard, semi-transparent spheres, which appear to be composed of a chitinous material. They are irregularly scattered, and may be sparse or so close together that they form hard masses.

*Colour.* According to the coloured sketch made by Professor Dakin, this species is of a deep chrome-yellow all over; the oral veil and branchial valves are of the same colour. There was apparently no trace of the black spots described by Eliot.

*Dimensions.* The specimens were all about the same size and measured when preserved 43 mm. long by 9 mm. wide by 10 mm. high; length of the tail-region 18 mm. Eliot's specimen was 33.5 mm. by 9 mm. by 12 mm.

*Head.* The head is small and in the specimens completely hidden between the front end of the foot and the overhanging oral veil. This veil is very well developed, and in all the specimens is tightly curled down over not only the head but also the anterior end of the foot.

*Foot.* The foot is fairly broad and lanceolate. The front end is rounded and the hinder end passes off to a point.

*Rhinophores.* The rhinophores are completely retractile within deep cavities. The aperture is in the form of an oval slit placed at an angle of about  $45^{\circ}$  to the main axis of the animal. At the posterior outer corner of the aperture lies a very large tubercle whose flap-like apex overhangs it.

*Branchiæ.* The branchiæ are fairly numerous, very small, and completely hidden by the three large valves. The three valves rise from a transverse ridge stretching across the middle of the back. The middle one passes back and curls downwards until it practically touches the dorsum. The lateral valves pass backwards, down and round partly forwards again, forming the commencement of a spiral. They also practically touch the dorsum. All

the valves, particularly the lateral ones, possess on their margins curious spatulate processes, which were described and figured by Eliot. The valves are very hard and bend over almost to touch the dorsum, so that the tiny gill-plumes, apparently arranged in three groups, cannot be seen without cutting off the valves.

*Labial Armature.* According to Eliot there is no labial armature, but in the specimens here described a circular ring of chitinous cuticle was present. It is not large and quite thin, but, nevertheless, it resisted boiling in potash solution and separated off from the lips as a distinct ring.

*Radula.* The radula contains no rachidial teeth. It is only moderately developed, and contains from 56-58 rows. The first row contained 18.0.18 (*i. e.*, 36 teeth), and the middle rows (34-42).0.(34-42), *i. e.* (68-84). The teeth are erect, moderately long, and slender, and so closely packed at the outside that they are difficult to count accurately. They are a little larger on the outside, but otherwise very similar throughout. Each consists of a more or less rectangular blade-like plate, one corner of which is carried on as a thin, slightly curved rod, bearing at its tip a small rounded secondary denticle. They are similar in general appearance, although differing in detail from those described by Bergh for *N. citrina* (11).

*Notes.* Three specimens were represented in the collection, and bore the label "1st Island. Shore Collecting. Outer side."

Professor Dakin, in his general account of the Abrolhos, says of this species:—"A straggling brilliant lemon-yellow sponge was one very evident specimen. After turning several stones over and noticing what appeared to be pieces of this sponge falling off, it was discovered that the falling pieces were Nudibranchs resembling the sponge both in colour and general appearance. The species belongs to the genus *Notodoris*, this being the first record for the genus on the Australian coast. It was instituted by Bergh for a single specimen of *N. citrina* from Rarotonga. Two other species have been made by Eliot for specimens from Zanzibar and the Maldivé Islands. All three are yellow in colour. It is stated in Eliot's report that nothing is known of the habits of these animals, and further:—"With Mr. Gardiner's specimen is a piece of hard yellow sponge. There is no note, but as the colour and consistency of the sponge closely resemble those of the Nudibranch it is highly probable that the latter frequent it."

"It is interesting to find that this is actually the case and in an entirely different region. Our specimens were always found associated with this sponge. The Nudibranch moves about slowly, so far as could be observed, and apparently lives in the dark under coral blocks."

This association between Nudibranch and sponge is not unknown, as witness the entirely different brilliant red Nudibranch *Rostanga pulchra* living on a similarly coloured sponge on the Pacific coast of North America (*vide* O'Donoghue, 60, p. 152).

As pointed out in the passage quoted above, only three species of this remarkable genus have been recorded : namely, *N. citrina* Bergh from Rarotonga by a single specimen, *N. minor* Eliot from Chuaka on the east coast of Zanzibar by a single specimen, and *N. gardineri* Eliot from the Maldiv Islands also by a single specimen.

In spite of certain minor differences, *i. e.* the presence of black spots, the presence of a Y-shaped arrangement of small tubercles on the dorsum, the absence of labial armature *inter alia* in Eliot's specimen, I have no hesitation in referring the present form to his species, *N. gardineri*. The size is about the same, the teeth similar, the valved rhinophoral aperture similar, and also the branchial valves with their elaborate spatulate processes.

As will be seen the genus is very little known, and it is to be hoped that sufficient material for a detailed investigation of its structure will be forthcoming. It apparently contains three distinct species :—

- N. CITRINA Bergh.—Pale yellow ; somewhat broader ; 7 quadripinnate gills ; gill-valve with 8 points more than one-third of the way forward ; valved rhinophoral aperture ; radula 56 rows typically 14.0.4, tooth with indication of third blunt denticle.
- N. GARDINERI Eliot.—Chrome-yellow with or without black spots, narrower ; numerous tiny gill-plumes ; gill-valves marked, three in number, furnished with spatulate processes, about halfway back ; valved rhinophoral aperture ; radula 56–58 rows typically (34–42).0.(34–42), tooth with only second blunt denticle.
- N. MINOR Eliot.—Lemon-yellow sharply marked with black lines, narrower ; 27 small tufts of gills in three areas ; gill-valves three in number, inconspicuous, simple ; radula 33 rows typically 25.0.25, tooth not nearly so distinctly denticulate as in foregoing species.

These differences appear to warrant the retention of the three forms as valid species.

Genus NEMBROTHA Bergh, Malakol. Unters. Ileft xi. p. 450 (1877).

Type here designated, *N. nigerrima* Bergh.

The body is limaciform, nearly smooth ; dorsum not differentiated from sides ; the rhinophores are retractile with a perfoliate clavus ; the branchiae are paucifoliate and bi- or tri-pinnate ; the tentacles are short and lobate ; the foot is quite narrow. The labial armature is inconspicuous or absent. The radula fairly narrow ; the rachidial tooth is depressed, subquadrate, or an armed curve ; the first pleural tooth is large and falciform, and the several external teeth are depressed.

The hermaphrodite gland is connate with the liver; no discrete prostate is present; the glans penis is armed.

There is a possibility that the generic name *Nembrotha* Bergh, 1877, will have to be replaced by *Angasiella* Angus & Cross, 1864: the form described by the latter being very much like those in Bergh's genus—indeed, Bergh himself includes it as a doubtful member of the genus. The matter can hardly be definitely settled unless the collection of further specimens renders it possible to examine it more closely.

Species *NEMBROTHA PURPUREOLINEATA*, sp. nov. (Pl. 28. figs. 16, 17; Pl. 30. figs. 60, 61.)

*Body.* The body is limaciform, rising from the front end to the middle, where it bears the branchiæ, thence it gets lower again and terminates in a short tail. The smooth dorsum passes over into the side of the body without line of demarcation or pallial edge. The anterior end bears a narrow veil-like expansion.

*Colour.* The general body-colour of the preserved animal is a dirty yellowish grey marked with pale brown lines. A broad dark band commences just behind the rhinophores and passes back in the mid-dorsal line to the branchiæ. A thinner dark line passes round the front, anterior to the rhinophores, and back on each side of the dorsum. Behind the branchiæ these two lines converge and meet, about halfway between the gills and the posterior end, to form one line in the middle which runs back to the end of the tail. Another line starts at the front end about halfway up the body on each side. It runs back roughly parallel with the edge of the foot to join the dorsal line near the tail. Professor Dakin informs me that in life the body-colour of the animal was a translucent slate-grey and the dark bands were purple-brown.

*Dimensions.* The form of the specimen was not well preserved, but it measured 35 mm. long by 10 mm. wide and 11 mm. high.

*Head.* The head is small and not conspicuous. At each side it bears a tiny tentacle, somewhat knob-shaped in the retracted condition, and between them is the circular mouth.

*Foot.* The foot is linear and not strongly developed. The hinder end passes off into the pointed tail, and the anterior end is cleft and has rounded corners.

*Rhinophores.* The rhinophores are small, have a perfoliate clavus, and are completely retractile within cavities with smooth round apertures.

*Branchiæ.* The non-retractile branchiæ consist of five bipinnate plumes, joined at their bases. The anterior one is in the middle line and larger than the others.

*Radula.* The radula is relatively small and when flattened measured 4 mm. by 2 mm. It bears 32 rows of teeth and the number in the oldest row is

7.1.1.1.7 (*i.e.*, 17) and in the newer portions 8.1.1.1.8 (*i.e.*, 19). The rachidial tooth is in the form of a broad irregular octagon with its posterior side uncurved and thicker in its anterior half. Its front edge is straight, but furnished with four curious papilliform denticles directed backwards—one of the inner of these bifid. In the radula of the specimen examined it was always the inner one on the same side. The first lateral has an irregular elongated base lying at an angle of about  $40^{\circ}$  to the middle line of the radula. It bears two very strong, backwardly directed, conical spines—one at its anterior end and the other about two-thirds of the way back. This is followed by a series of teeth, seven or eight in number. They take the form of approximately square plates in the inner teeth, but become oblong and less strong towards the outside.

*Labial Armature.* The lips are furnished with a lining of thin chitin, which has an oval opening, whose long axis is vertical.

The anus lies on a short rounded papilla in the middle line behind the junction of the bases of the posterior branchial plumes.

The genital aperture lies near the anterior end in the light space between the two lateral dark bands and about halfway between the head and the branchiae.

*Notes.* The species is represented by one specimen, which was taken on the Abrolhos, but with no details of the exact locality.

In spite of the presence of a labial cuticle rather more strongly developed than in other forms, there is no doubt that this belongs to the genus *Nembrotha*. It does not appear to agree with any previously described.

#### A COPEPOD PARASITIC ON *CERATOSOMA BREVICAUDATUM*.

The presence of Copepoda parasitic upon Nudibranchs has been reported by several authorities. The first record is apparently that of Leydig (56), in 1853, who constituted the genus *Doridicola* for Copepods found on Dorids. Similar forms are also reported by Alder and Hancock (5) from *Archidoris tuberculata* and *Antiopa cristata*, and they were referred to the genus *Ergasilus*, although they were probably congeneric, if not even conspecific, with Leydig's forms, as was pointed out later by Hancock and Norman (47). They are not highly modified animals and apparently more in the nature of epizootic forms, and their parasitism has not been proved.

In addition to these, however, a group of highly specialised forms, undoubtedly parasitic, have also been described. The first, reported by Hancock and Norman (47), are:—*Splanchnotrophus gracilis*, parasitic on *Acanthodoris pilosa* and *Idalia aspersa* from the English coast, and *S. brevipes*, parasitic on *Doto coronata* and *Coryphella rufibranchialis* also from the English coast. The only other authority that has dealt with these parasites is R. Bergh, who has recorded the following:—

Parasite.	Host.	Locality and Reference.
<i>Splanchnotrophus brevipes.</i>	<i>Galvina viridula.</i>	North Sea (21, p. 568).
<i>Splanchnotrophus</i> sp.	<i>Coryphella rufibranchialis.</i>	Norway (21, p. 568).
<i>Ismatia monstrosa.</i>	<i>Phiduna lynceus.</i>	W. Coast, S. America (9).
" "	" <i>inca</i>	W. Coast, S. America (26).
" "	<i>Archidoris incerta.</i>	W. Coast, S. America (26).
<i>Ismatia</i> sp.	<i>Lomanotus</i> gener.	Mediterranean (21, p. 568).
<i>Briarella microcephala.</i>	<i>Ceratosoma trilobata.</i>	Red Sea (13, p. 409).
<i>Briarella</i> sp. probably.	<i>Glossodoris elisabethina.</i>	Philippines (16, p. 472).
<i>B. microcephala.</i>	<i>Asteronotus hertrana.</i>	Philippines (19, p. 641).

The total number of species is very small, only four named for certain and a possibility of seven at the most, and, from the infrequency with which they have been recorded, it would appear that they are rare. Indeed, in many hundreds of specimens I have handled from British Columbia, I have not yet encountered one. In spite of this, however, it will be seen from the above list that they are widely distributed over the world. The following form is of interest, not only on its own account, as a new species of a rare group, but also because it shows that the group also extends to the Australian seas.

#### Family CHONDRACANTHIDÆ.

Genus *SPLANCHNOTROPHUS* Hanc. & Norm. Trans. Linn. Soc. Lond.  
xxiv. 1864, p. 51.

Type here designated : *S. gracilis* Hanc. & Norm. l. c. p. 51.  
Coast of England.

*Female.* Head and thorax either blended into a single segment, the thoracic portion of which is furnished on each side with unarticulated arm-like appendages or lobes, or the first part only of the thorax is united with the head and the last part forms a second, but comparatively minute, segment. In this case, however, all the thoracic appendages are attached to the first segment. First antennæ minute and few-jointed; second larger, in the form of prehensile hooks. Labrum large, overhanging the mandibles, which organs, together with the maxillæ and two pairs of foot-jaws, are minute and crowded round the mouth. Thoracic feet two pairs, minute, simple or two-branched, terminating in hooks. Abdomen two-jointed, the last joint ending in two caudal appendages, which are furnished with one or two simple setæ. Ovipigerous sacs elliptical.

*Male* minute. Cephalothorax with lateral appendages and divided into four segments, the first of which bears two pairs of thoracic feet.

Species *SPLANCHNOTROPHUS MACCULATUS*, sp. nov. (Pl. 30. figs. 65, 66.)

*Female.* The body is elongated and roughly cylindrical, but slightly depressed dorso-ventrally, and it is encased in a thin, not very strong, layer of semi-transparent chitin. It is composed of a cephalothorax, of which the anterior portion is the head, but it is not distinctly marked off from the thorax, and a much smaller abdomen. On the dorsal surface of the cephalothorax are three sac-like outbulgings of the body-wall. The first of these is in the form of a transverse collar-like ridge right across the body, and it is somewhat firmer than the other two. The second is much larger, more inflated, and more irregular. The anterior border and the lateral lobes of it are sharply marked off from the body, but in the mid-dorsal region the hinder parts of the two lateral lobes merge with the general surface of the body. The third sac is, if anything, larger than the second, and its lateral lobes show a slight marginal indentation.

The last portion of the thorax is narrower than that in front, but it swells out towards its hinder edge and then rapidly narrows again still further to the point where it joins the abdomen.

From the ventro-lateral aspects of the cephalothorax arise three pairs of long, tapering, cylindrical outgrowths. The first pair arise at a level between the first and second dorsal sacs. The second pair arise at a level between the second and third dorsal sacs, and the third pair touch the second and are level with the third dorsal sac. These lateral outgrowths are not, as might be supposed at first sight, modified appendages, for the rudiments of these lie on the ventral surface, but they are outgrowths of the body-wall. They are very conspicuous, as they almost double the length of the animal itself, and apparently are concerned with the absorption of nutritive material from the host, since they lie in the spaces between the viscera.

Strings of eggs, either in single or double rows, show through the body-wall and form a network of interlacing lines in the various parts of the cephalothorax, the dorsal sacs, and the basal portions of the long outgrowths.

The first antennæ are a pair of minute, stumpy, seemingly uniramous appendages lying under the head a short distance from the anterior end. Each is apparently composed of three joints and bears a number of relatively stout spines; there are three of these on the basal joint, two on the next, and two on the terminal joint. The second antennæ, while still small, are considerably larger than the first, and are plump, fleshy, uniramous appendages also showing indications of three joints. They are relatively shorter than the corresponding members in *S. gracilis*. Stout spines are also present on these: two on the basal joint, one on the next, and two on the terminal joint.

The labrum is large, curved ventrally, and sub-triangular in shape with a rounded apex and a deep curved indentation in the base. The mouth presumably lies under this indentation. The mandibles are small and consist of



a soft triangular base, which bears at its antero-median corner a small stiff blade with three denticles. The maxillæ are very small triangular lobes partly hidden by the mandibles. Each bears a spine-like prolongation at its antero-median corner. The first maxillipedes are somewhat triangular in shape, not unlike the mandibles, save that in place of the blades they bear spine-like processes. The second maxillipedes are long thin structures, expanded dorso-ventrally in their anterior region, and bearing spine-like prolongations at the anterior end. They are approximated in the mid-ventral line over the front part of their length, but diverge posteriorly. Altogether the mouth-parts show a considerable resemblance to those of *S. gracilis*, but their proportions are different, and they appear to be a little more degenerate.

On the ventral side of the cephalothorax there are a pair of rounded papilliform processes opposite the bases of the first lateral appendages, and another and quite similar pair opposite the ends of the last pair of lateral outgrowths. These are in the same relative position as the tiny legs in *S. gracilis*, as shown in the drawing of Hancock and Norman, but, while each bears a small spine, they are not nearly so much like thoracic appendages as those of *S. gracilis*.

If we adopt the interpretation given by Hancock and Norman (47, p. 52), two regions can be distinguished in the abdomen: the first an inverted cone joining on to the posterior end of the cephalothorax and the second another inverted cone with a rounded edge at the base borne on the preceding part. This second cone has a firmer chitinous covering than the cephalothorax and bears four annular grooves; thus it is divided up into five rings, but whether these represent actual abdominal segments or not it is hardly possible to say. Hancock and Norman group the anterior cone-shaped portion together with the basal ring of the second cone as the first complete abdominal segment, although in the present species there is a distinct, annular, articular groove separating them. The basal ring of the second cone-shaped portion has two lateral projections upon which the egg-sacs are borne. On the terminal portion of the abdomen are two small cylindrical projections each terminating in a short spine.

The egg-sacs are elongated, cylindrical, soft-walled sacs with rounded ends. The sacs measured, in one individual, 6.2 mm. long by 1.2 mm. wide. The eggs within them are apparently just crowded together without definite arrangement, as is characteristic of the family Chondranchthidæ, and do not exhibit the linear arrangement that is found in the Caligidæ.

*Notes.* Two specimens of this species were found upon one individual of *C. brevicaudatum*, both female and about the same size. The one of these measured 8.5 mm. long by 4.1 mm. broad; its egg-sacs, as noted above, were 6.2 mm. long by 1.2 mm. wide and the length of the longest lateral process was 14.75 mm. One specimen was partially embedded in an actual hole in the body-wall of the Nudibranch about 5 mm. behind the urinary aperture,

and looked as if it were in the process of boring its way down to get into the body-cavity. This specimen was very noticeable from the outside, and its long lateral appendages and most of the body projected freely from the dorsal surface of its host. In examining this individual it was noticed that two peculiar sac-like structures containing eggs of a deep golden-yellow colour were projecting from the much dilated renal pore. Further examination and dissection revealed the presence of a second and slightly larger example of the parasite completely hidden within the body of the host—the measurements of this specimen are given above. It was lying within the renal duct at its posterior end, but it was so large and its lateral arm-like appendages spread about so much among the viscera that it was not possible to see whether the animal was completely confined within the renal duct, which had become enormously dilated and ramified, or whether it had broken through the wall of this structure.

While the specimen on the outside of the Nudibranch contained eggs within the body, visible through the semitransparent body-wall as a tracery of lines, it showed no sign of egg-sacs. If these had not been torn off, therefore, it would appear as if the production of eggs had not proceeded far in this individual. In the second specimen, on the other hand, egg-sacs were present and of large size. As noted above, they projected through the renal pore, which was much enlarged or perhaps actually broken, and also projected through the partially closed branchial aperture. They were extremely thin-walled and delicate, and in the subsequent process of excavating the ramifications of the parasite from the body of the host they were badly broken up—fortunately not until after they had been measured. When the branchiae were expanded, the egg-sacs must have lain among the branchial plumes as described in *S. gracilis*. The body of this individual also contained a number of eggs showing through the body-wall, and arranged in a series of inter-lacing lines which passed out into the lateral processes.

No trace of a male individual was found either on or near the females, or upon or in the body of the host. This is rather remarkable in view of the fact that Hancock and Norman state that the males, sometimes to the number of a dozen, are generally to be found associated with the females.

The present species is undoubtedly congeneric with *S. gracilis* Hancock and Norman, and quite similar to it in a number of ways. It differs in a number of points, however: the presence of the dorsal sacs, the segmentation of the abdomen, the more degenerate condition of the thoracic limbs, the greater length of the lateral appendages, and certain differences in the mouth-parts *inter alia*, and so it is here listed as a new species under the name *Splanchnotrophus sacculatus*. It is interesting to find a form from the Antipodes so closely allied to *S. gracilis*, heretofore only recorded from the European seas.

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## EXPLANATION OF THE PLATES.

## PLATE 27.

The photographs on this plate were all taken by Mr. Herring, of the British Museum.

- Fig. 1. *Tethys gigantea* (Sowerby). Dorsal aspect,  $\times$  about  $2/3$ . The large expanded lobes at the anterior end of the foot and the anal funnel are clearly shown.
- Fig. 2. *Tethys denisoni* (Smith). Dorsal aspect,  $\times$  1. The anal funnel in this specimen is folded in.
- Fig. 3. *Dolabriferu pelsartensis*, sp. nov. Dorsal aspect,  $\times$  1.
- Fig. 4. *Placobranchus expansa*, sp. nov. Dorsal aspect,  $\times$  1. The anterior extension of the mantle lobe in front of the flattened head shows clearly on the right side, but is torn and folded on the left. The anterior end of the head with the tentacles is withdrawn and does not show. The tiny pericardial swelling appears just behind the head. Owing to the shadow produced by lighting, a false impression of a solid body is given. In reality this region is mainly composed of the mantle lobes, and the actual body is not quite as wide as the head; it cannot be distinguished from the lobes.
- Fig. 5. *Sphaerostoma dakeni*, sp. nov. Ventral aspect,  $\times$  1. The mouth shows as a longitudinal cleft at the anterior end, and part of the oral veil with one projection appears on the left-hand side. The margins of the foot in this specimen are almost approximated. Some of the large branchiæ show clearly on each side.
- Fig. 6. *Alloiodoris hedleyi*, sp. nov. Dorsal aspect,  $\times$  1. The granulate appearance of the back and the nature of the branchial and rhinophoral apertures are clearly visible.
7. — Ventral aspect of the specimen illustrated in fig. 6,  $\times$  1. The tiny head is not visible.
- Fig. 8. *Glossodoris westraliensis*, sp. nov. Dorsal aspect,  $\times$  1. The dark band near the margin of the notæum shows faintly.
9. — Lateral aspect,  $\times$  1. The broad dark band on the side of the body and the narrow one on the upper edge of the flange of the foot are visible. The front end of the foot is clearly bilabiate.
- Fig. 10. *Aphelodoris affinis* Eliot. Dorsal aspect,  $\times$  1. In places the darker line around the notæum is seen, and the dark-coloured branchiæ show in the circular spot towards the posterior end.

## PLATE 28.

The photographs on this plate were all taken by Mr. Herring, of the British Museum.

- Fig. 11. *Hexabranchus imperialis* Kent. Dorsal aspect,  $\times$   $2/3$ . The branchiæ and the clavus of the right rhinophore are clearly visible, and the relatively enormous size of the mantle folds can easily be judged.
- Fig. 12. *Asteronotus fuscus*, sp. nov. Dorsal aspect,  $\times$  1. This shows the ridges in the central region of the dorsum.
13. — Ventral aspect of the specimen illustrated in fig. 12,  $\times$  1. The relative sizes of the foot and mantle show clearly. The indentation at the posterior end is where a portion of the mantle has been broken away.
- Fig. 14. *Ceratosoma brevicaudatum* Abraham. Dorsal aspect,  $\times$  1. The tail is bent to the right, otherwise this gives a good idea of the shape of the animal and also the position of the rhinophoral and branchial apertures and the tongue-like prolongation of the dorsum.

- Fig. 15. *Dendrodoris mammosa* (Abraham). Dorsal aspect,  $\times 1$ . While the general appearance is shown well there is no indication of the colour-markings.
- Fig. 16. *Nembrotha purpureolineata*, sp. nov. Dorsal aspect,  $\times 1$ . This indicates the general form of the animal, save that the tail is turned to the right, and also the position of the branchiæ.
17. — Lateral aspect of the specimen illustrated in fig. 16,  $\times 1$ . This shows the way in which the body increases in height to the level of the gills and then falls away to the tail.
- Fig. 18. *Notodoris gardineri* Eliot. Dorsal aspect,  $\times 1$ . The general form of the body with the tail turned to the right: the rhinophoral apertures and the branchial valves are clearly shown.
19. — Lateral aspect,  $\times 1$ . The tail in this specimen is turned up. It shows clearly the rough nature of the surface, the large size of the branchial valves, and here and there some of the hard spheres.

## PLATE 29.

All the figures on this plate were drawn from preparations from specimens in the collection and at the various magnifications shown by the aid of a camera lucida.

- Fig. 20. *Tethys gigantea* (Sowerby). The median tooth and first two pleural teeth of one side,  $\times 97$ .
21. — Three pleural teeth from near the middle of the row,  $\times 97$ .
22. — The six outermost pleural teeth,  $\times 97$ .
- Fig. 23. *Tethys denisoni* (Smith). The median tooth and first two pleural teeth of one side,  $\times 97$ .
24. — Three pleurals from near the middle of the row,  $\times 97$ .
25. — The seven outermost pleurals,  $\times 97$ .
- Fig. 26. *Dolabrifera pelsartensis*, sp. nov. The median tooth and first two pleural teeth of each side,  $\times 97$ .
27. — Three pleurals from near the middle of the row,  $\times 97$ .
28. — The four outermost pleurals,  $\times 97$ .
- Fig. 29. *Berthella plumula* (Montagu). The two innermost pleurals,  $\times 250$ .
30. — Two pleurals from near the middle of the row,  $\times 250$ .
- Fig. 31. *Placobranchius expansa*, sp. nov. Three teeth near the inner end of the radula, seen from the side,  $\times 190$ .
32. — A single tooth from near the outer end of the radula, seen from the side,  $\times 190$ .
33. — A single tooth from near the outer end of the radula, seen from above,  $\times 190$ .
34. — A single tooth from the sac, seen from the side to show the relatively small size,  $\times 190$ .
- Fig. 35. *Sphaerostoma dakeni*, sp. nov. The jaws, antero-ventral view,  $\times 3$ .
36. — The jaw, lateral view,  $\times 3$ .
37. — Two rows of the median tooth and the first pleural tooth on each side,  $\times 97$ .
38. — The four pleurals next to the innermost pleural,  $\times 97$ .
39. — Three pleurals from near the middle of the row,  $\times 97$ .
40. — Three outermost pleurals,  $\times 97$ .
- Fig. 41. *Hexabranchius imperialis* Kent. The four innermost pleurals,  $\times 70$ .
42. — The fourth pleural, side view,  $\times 70$ .
43. — Three pleurals from near the middle of the row,  $\times 70$ .
44. — Four outermost pleurals,  $\times 70$ .

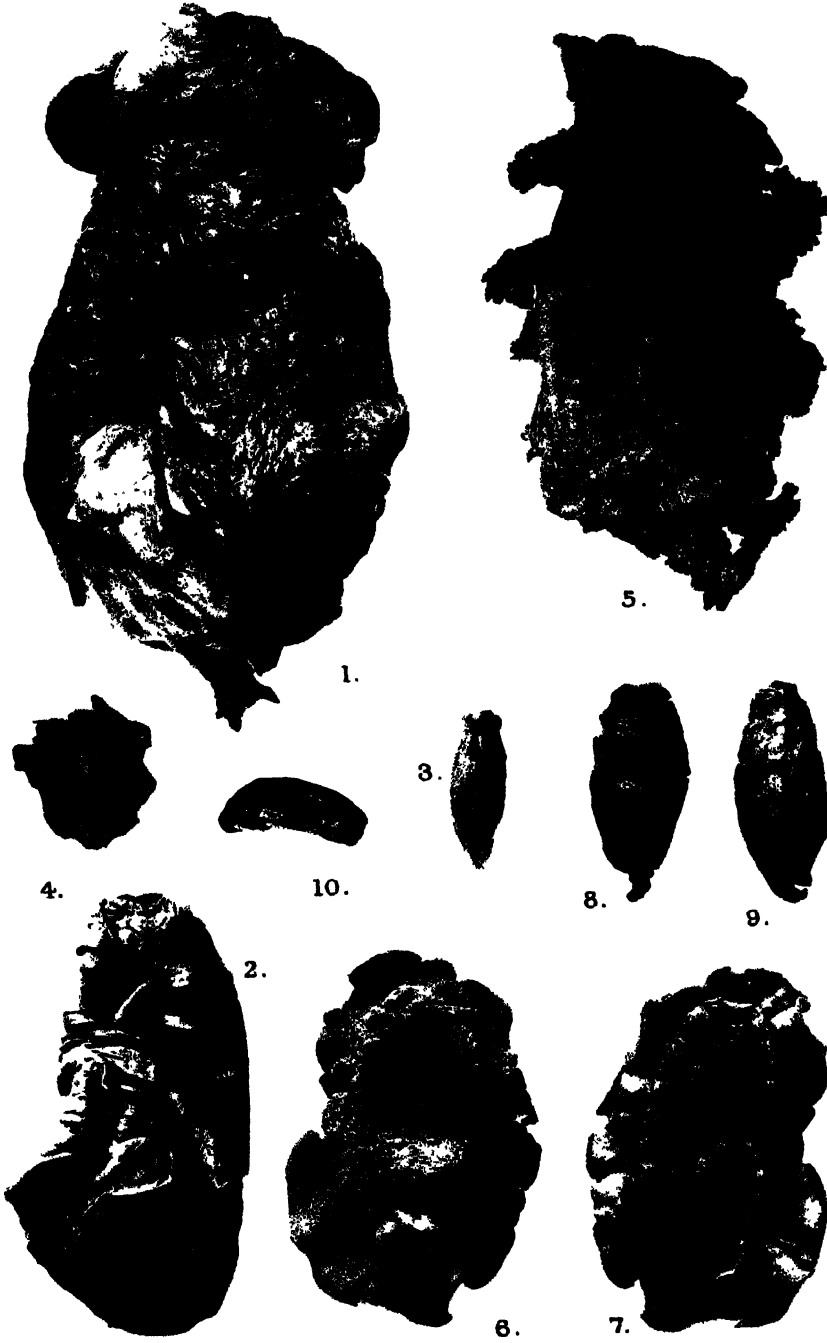
PLATE 30.

All the figures on this plate were drawn from preparations from specimens in the collection and at the various magnifications shown by the aid of a camera lucida.

- Fig. 45. *Alloiodoris hedleyi*, sp. nov. The four innermost pleurals,  $\times 97$ .  
 46. — Four pleurals from near the middle of the row,  $\times 97$ .  
 47. — The four outermost pleurals,  $\times 97$ .  
 Fig. 48. *Asteronotus fuscus*, sp. nov. The three innermost pleurals,  $\times 150$ .  
 49. — Three pleurals from near the middle of the row,  $\times 150$ .  
 50. — The five outermost pleurals,  $\times 150$ .  
 Fig. 51. *Glosiodoris vestraliensis*, sp. nov. The four innermost pleurals, lateral aspect,  $\times 162$ .  
 52. — Three pleurals from near the middle of the row, lateral aspect,  $\times 162$ .  
 53. — Three outermost pleurals, lateral aspect,  $\times 162$ .  
 Fig. 54. *Aphelodoris affinis* Eliot. The four innermost pleurals,  $\times 150$ .  
 55. — Two pleurals from near the middle of the row,  $\times 150$ .  
 56. — The five outermost pleurals,  $\times 150$ .  
 Fig. 57. *Ceratosoma brevicaudatum* Abraham. The four innermost pleurals,  $\times 97$ .  
 58. — Four pleurals from near the middle of the row,  $\times 97$ .  
 59. — The five outermost pleurals,  $\times 97$ .  
 Fig. 60. *Nembrotha purpureolineata*, sp. nov. The labial cuticle, lateral aspect,  $\times 10$ .  
 61. — The rachidial tooth and the pleurals of one side,  $\times 97$ .  
 Fig. 62. *Notodoris gardineri* Eliot. Labial cuticle, front view,  $\times 10$ .  
 63. — Four inner pleurals, lateral aspect,  $\times 97$ .  
 64. — The four outermost pleurals, lateral aspect,  $\times 97$ .  
 Fig. 65. *Splanchnotrophus sacculatus*, sp. nov. Dorsal aspect,  $\times 5$ . D.S. Dorsal sac;  
 E.L. Line of eggs; E.S. Egg-sac; L.A. Lateral appendage.  
 66. — Ventral view of the mouth-parts,  $\times 62$ . The parts are somewhat distorted  
 by the pressure of the cover-glass, and the first antenna on the left side of the  
 drawing has been turned forwards. 1 A. First antenna; 2 A. Second antenna;  
 L. Labrum; M. Mandible; 1 Mp. First maxillipede; 2 Mp. Second maxilli-  
 pede; Mx. First maxilla.



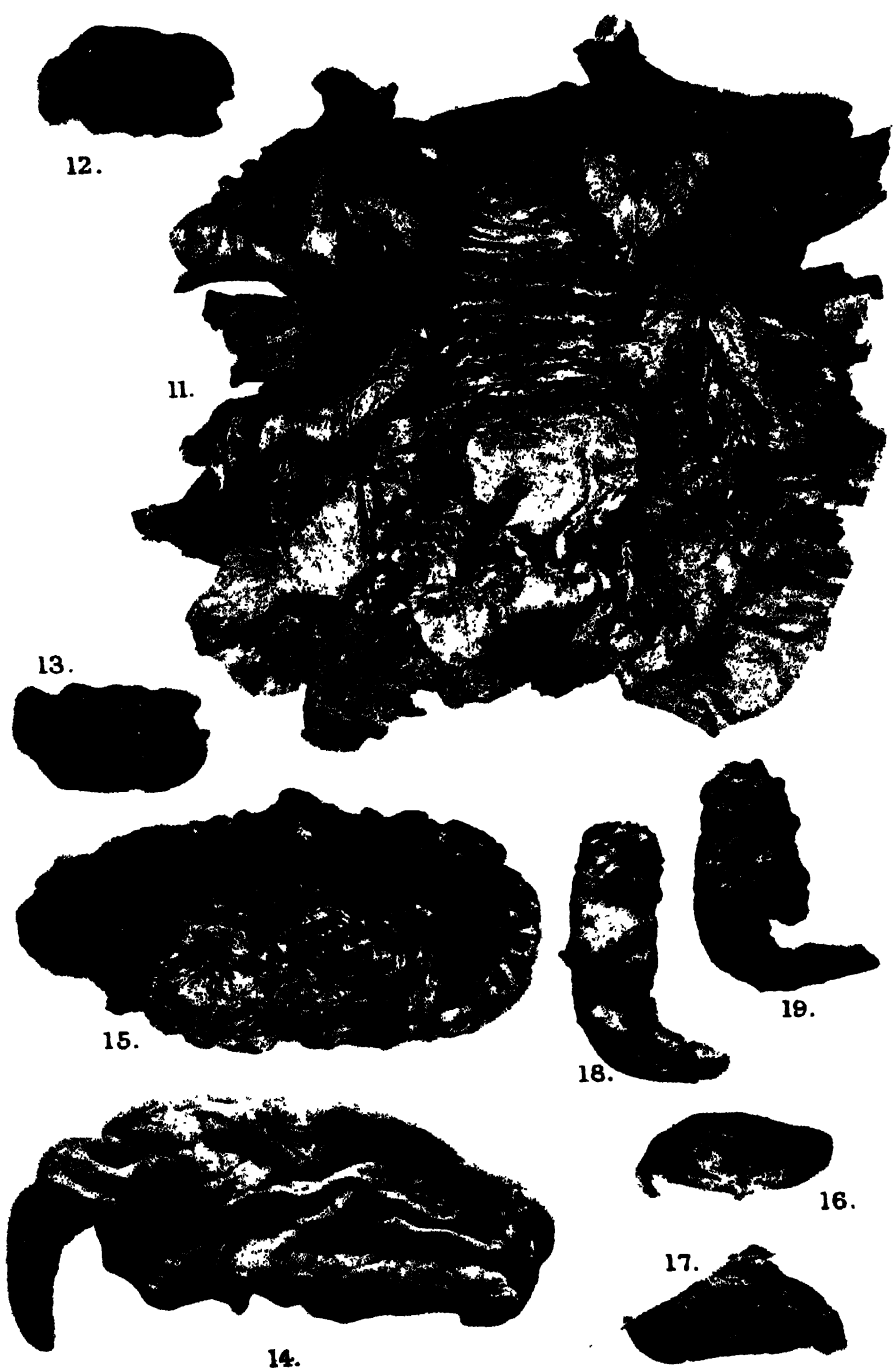




Muth coll

ABROLHOS OPISTHOBRANCHIA.

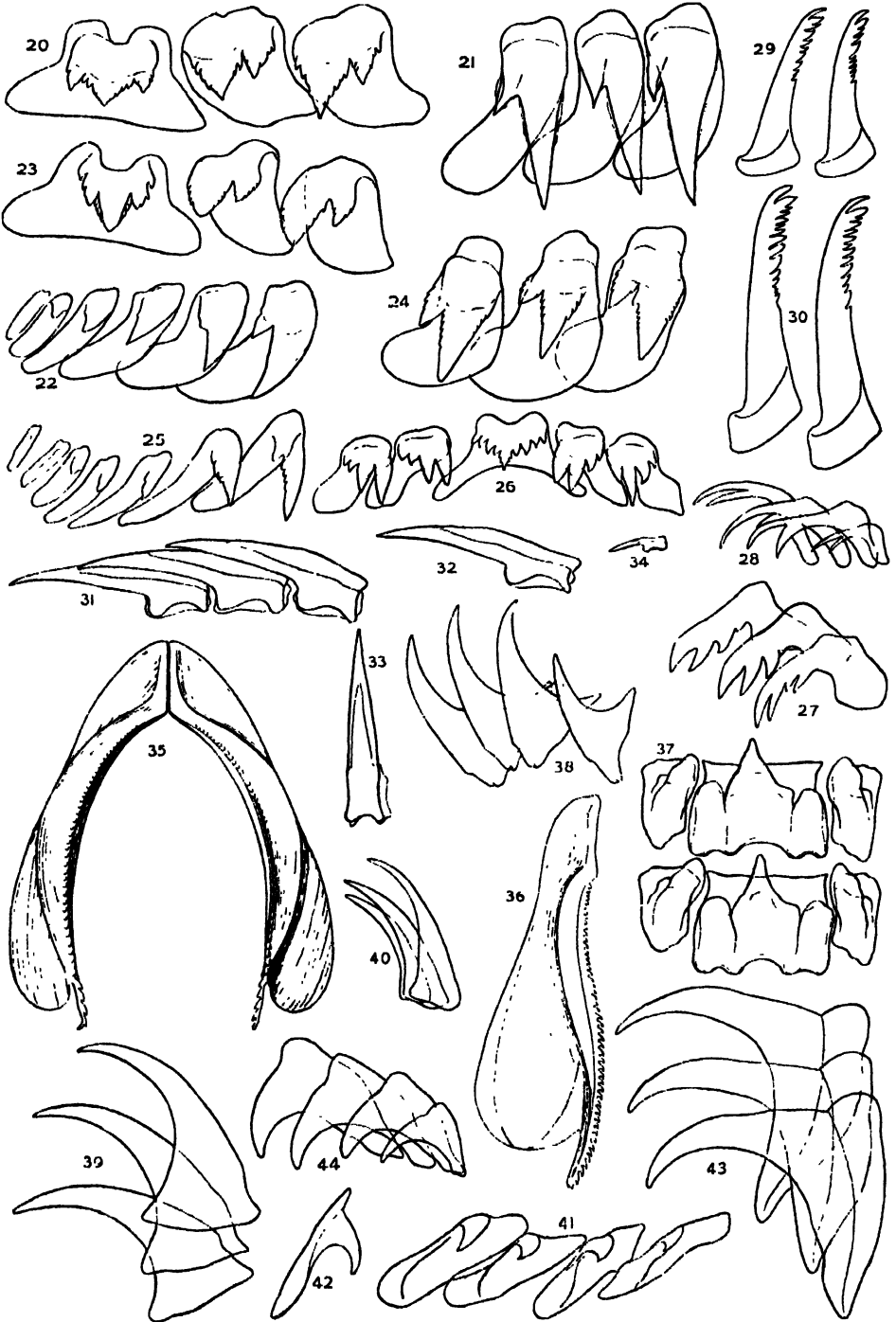




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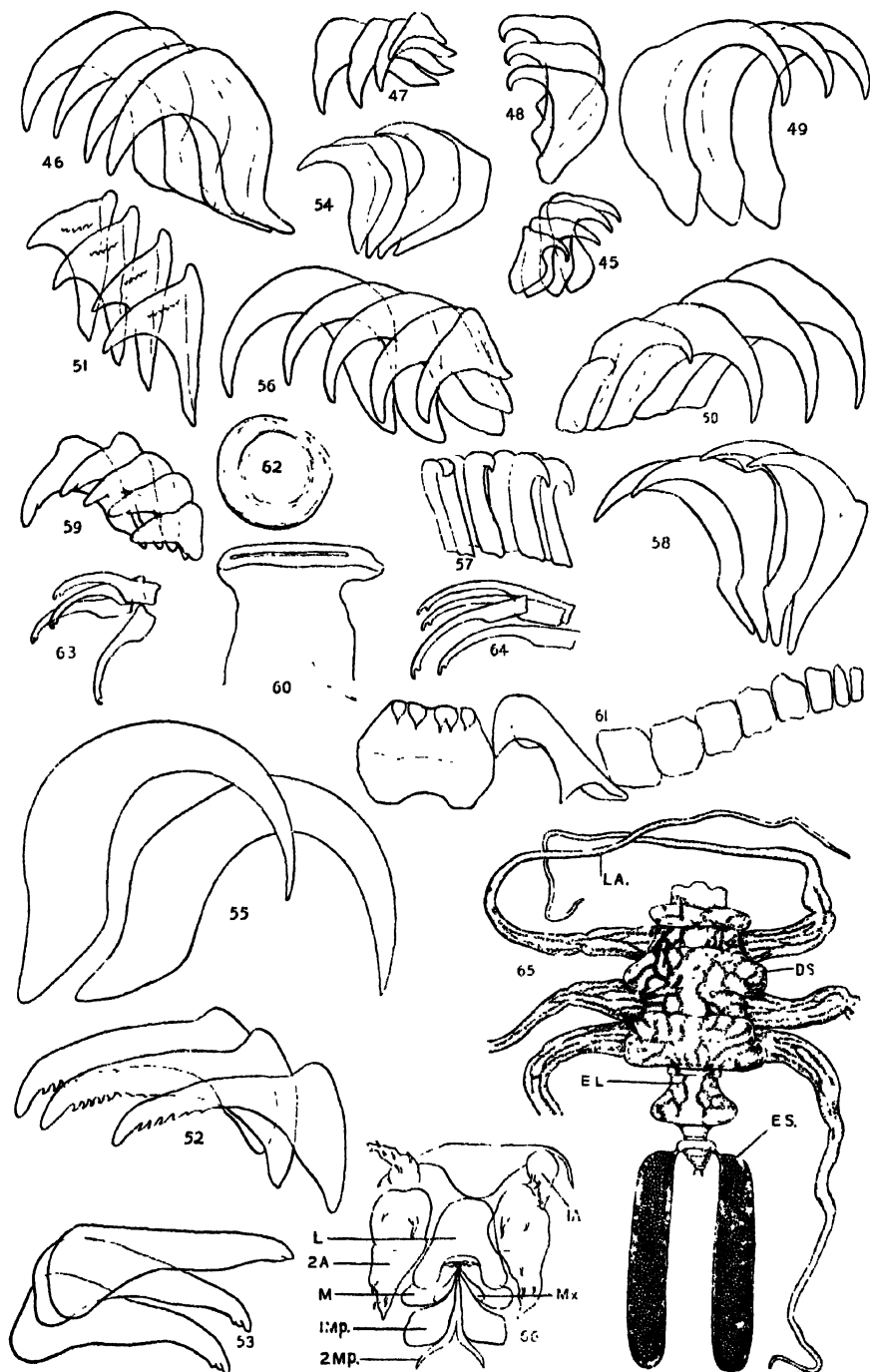
ABROLHOS OPISTHOBRANCHIA.





OPISTHOBRANCHIATA FROM THE ABROLHOS ISLANDS.





OPISTHOBRANCHIATA FROM THE ABROLHOS ISLANDS.





On the Genital System of *Lyctus brunneus* Steph., with a Note on *Lyctus lineatus* Goeze (Coleoptera). By A. M. ALTSON, F.E.S. (Continued by Dr. A. D. JAMES, F.L.S.)

(PLATES 31-34, and Text-figures 1-4.)

[Read 3rd May, 1923.]

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INTRODUCTION.

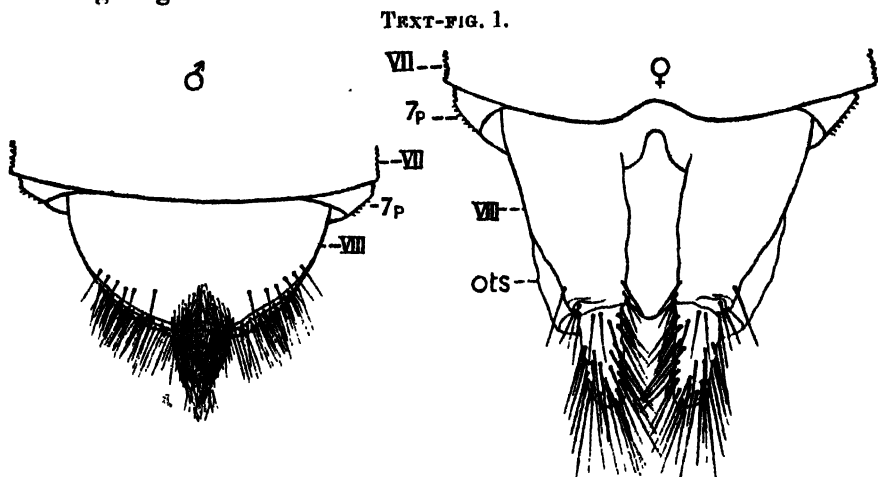
In the following description of the genital system of *Lyctus brunneus* Steph., it has been found necessary to add a comparative description of part of the alimentary tract of both sexes: that of the male discloses nothing remarkable in the position of these parts, whereas that of the female is curiously situated, and appears to be only partially adapted to meet its particular method of oviposition.

Sharp and Mjör (10) figure and describe the male genital tube of *L. lineatus* Goeze (*conduplicatus* Fab.). Other than this, no reference to the genital system of either sex of any species of *Lyctus* has been found.

To complete the examination of the organs of the female *L. brunneus*, it was necessary to cut series of sections. Longitudinal and transverse sections were made of pupae, immature and mature adults. Immature adults refers to beetles removed from their pupal chambers before either their integument had hardened or they had eaten any wood, *i. e.* between four and five days after shedding the pupal exuviae.

The beetle are not sexually mature until they are ready to emerge, and emergence invariably takes place at the earliest possible opportunity after that

The only secondary sexual characters observed were a difference between the ventral pygidial plates (VIII sternite) and between the apical margins of sternites VII (the 5th visible sternite of systematists) (text-fig. 1). Beyond these characters, unless the "ovipositor" or the œdeagus is extruded, or a pair are found in coition, it is impossible to distinguish the sexes externally, size being no guide.



Secondary sexual characters of *L. brunneus*. Male and female ventral pygidial plates. *ots*, base of outer sheath of ovipositor; VII, 7th sternite; 7p, 7th pleurite; VIII, 8th sternite. *Camera lucida*,  $\times 250$ .

In the description of the male genital tube the nomenclature of Sharp and Muir (10) is followed, but in the case of the female reference was made to Packard (8), Berlese (2), Henneguy (3), and Stein (11) for terms applied to parts homologous to those found in *L. brunneus*.

#### TECHNIQUE AND METHODS.

The technique adopted to prepare the specimens for sectioning was similar to that employed by Awati (1). This method gave excellent results.

Fixation in Carnoy II for 24 hours; three to four hours after immersion in the fixative the head and most of the legs and the elytra and wings were cut off.

Dehydration in two washings of 90 per cent. alcohol, three hours; two washings in absolute alcohol, three hours; and one hour in a mixture of chloroform and absolute alcohol.

The object was next transferred to chloroform, in which it remained for two days; then into a cold saturated solution of paraffin-wax (58° C.) in chloroform, where it remained for two to three days. After this period the solution was warmed by standing it on top of the oven for 10 minutes, and the object was then transferred into pure molten wax (58° C.) for five to six hours.

A block was prepared in the usual way. The sections were stained in Ehrlich's Hæmatoxylin ( $\frac{1}{2}$  hr.) and counter-stained in Picro-nigrosin (30 secs.).

#### MALE GENITAL SYSTEM.

The reproductive organs are shown in Pl. 31. fig. 1, and consist of the usual parts: testes (*ts*), vasa deferentia (*vd*), seminal vesicles (*sv*), accessory glands (*ag*), ejaculatory duct (*ej*), internal sac, median lobe (*ml*), and tegmen, comprising the lateral lobes (*ll*) and basal piece (*bp*).

There are six testicular follicles of unequal size attached to each vas deferens. They occupy a large area in the abdomen from the dorsal to the ventral surface, and extend from beyond the basal margin of the abdomen to the third sternite (Pl. 31. fig. 5). The testicular follicles are white, rounded and tapering towards their apex. There is a slight cavity in the centre of the base of each, whence a tube arises which joins the vas deferens, which is of variable thickness throughout its length. In repose the vasa deferentia are convoluted, in parts superimposed, and lie on the ventral surface. The vasa deferentia enter the seminal vesicles on their outer ventro-lateral margin (Pl. 31. fig. 4). The seminal vesicles are joined on their inner lateral surface for the greater part of their length; they are subcylindrical and rounded at their apices.

Arising from each seminal vesicle on its inner dorsal margin is a short tube; these tubes meet and form the ejaculatory duct. Superimposed and attached to the dorsal surface of each of the two short tubes is an accessory gland. The accessory glands are subcylindrical and curved, broadest towards their base and rounded at their apices.

The ejaculatory duct gradually tapers from its base until it enters the median lobe through the median foramen (*mf*), where it becomes hidden from view, emptying into the internal sac (*is*, Pl. 31. fig. 3). (It was not found possible to evaginate the internal sac, nor to kill a pair of beetles in coition with the organs *in situ*; but the internal sac was traced in sections of an immature male.)

The chitinized median lobe, viewed in section, is circular at its base and shortly becomes elliptical; towards its apex there arise on the upper dorsal and upper ventral surfaces a carina situated along the centre, with the internal sac lying over and on either side of the carina formed on the upper ventral surface (Pl. 31. fig. 2); the lower or outer ventral surface is convex at this point. The median orifice (*mo*, Pl. 31. fig. 3) is situated a little below the upturned point of the median lobe. Inside the median lobe are series of muscles and nerve-fibres (Pl. 31. fig. 2); one series of muscles is situated around the internal sac, others are attached to the walls of the lobe.

Encasing the median lobe on either side are the lateral lobes, which are roughly semicircular in section for the greater part of their length; they are

of a uniform thickness of chitin except towards their base, where the inner face becomes thin and flexible. Each lateral lobe contains a group of muscles and nerve-fibres extending to their apices (Pl. 31. fig. 2). At their base the lateral lobes become joined together ventrally and dorsally; at the latter point they join around the point of articulation (*pa*). Externally the median lobe and the lateral lobes bear sensory pits at their apices.

Enclosing the base of the lateral lobes is a thin piece of chitin, the basal piece (*bp*), which appears to clip the dorsal edges of the lateral lobes below the point of articulation. Arising from the surface of the basal piece towards its posterior margin is the flexible enveloping integument of the abdomen.

In sections of a male the spermatozoa were found in bundles, held together at their heads. In balsam mounts of the dissected genitalia these bundles could also be seen within the testicular follicles when the organs had been stained in hæmalum and indigo-carmin.

Between the dorsal pygidial plate (*dp*) and the œdeagus is a chitinous tube (*ev*) which completely envelops the anus (*an*) and anterior portion of the rectum (*r*) (Pl. 31. figs. 2 & 3). Each side of the chitinous tube (*ev*) invaginates to form a pair of stout rods (*vr*, fig. 3). These rods surround the œdeagus and abut at their base, which is towards the ventral surface of the abdomen. From the base of the rods there are three primary sets of muscles (*m*). Two of these sets follow the course of the rods and terminate around the chitinous tube; the third set runs between the rods and is attached to the enveloping integument below the base of the œdeagus; some of these muscles appear to be attached to the œdeagus ventrally.

From this it would appear that the latter muscles are primarily responsible for giving the œdeagus its necessary downward tilt preparatory to coition.

Following the alimentary tract back from the anus (*an*, Pl. 31. fig. 5) is the rectum (*r*), which is quite short and lies dorsal to the œdeagus and ejaculatory duct. Beyond the rectum is the colon (*cl*) lying dorsal to the accessory glands, part of the ejaculatory duct, and the seminal vesicles. Beyond the colon is the ileum, which disappears below the testicular follicles and lies towards the ventral surface of the abdomen. There are six malpighian tubes (*mp*) arising from the ileum, which at this point is lined with chitinized setæ. Beyond the ileum is the mesenteron (*ms*), which lies in the meta- and mesosternum, where it inclines towards the dorsal surface.

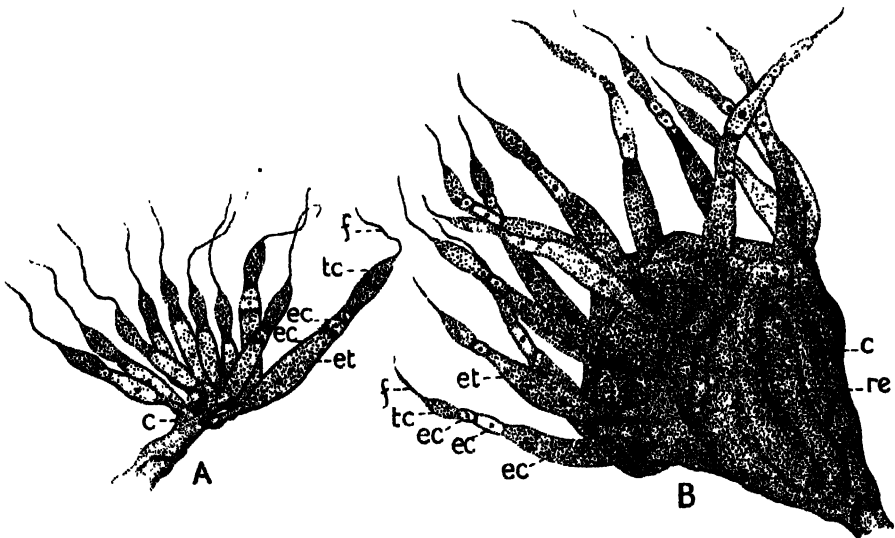
Arising from between the metathoracic acetabula (*mta*) is a "U"-shaped, strongly chitinized apodeme (*ap*); the base of the "U" arises from the metasternum (*g*), whilst the apices of the arms are held in position by muscles attached to the metanotum. From inside the "U"-piece and from its base arise two thin chitinous rods (*apr*). These rods traverse the floor of the metasternum and terminate above the metathoracic coxæ (*mc*), to which they are attached by radiating muscle-fibres.

A pair of glands or sacs (*sg*) disappearing beneath the *œdeagus* (*oe*) are shown (Pl. 31. figs. 1, 3, & 5). These glands unite and form a short narrow duct. When dissected out of a mature beetle the glands and duct are always found distended. The duct terminates abruptly between the 7th and 8th sternites. In section these glands are seen to be composed of cells containing very large nuclei. The function of the glands is not known; no odour other than that of the wood from which the beetles emerged was ever perceived. The glands are apparently pygidial glands (Berlese 2).

#### FEMALE GENITAL SYSTEM.

The reproductive organs of the female (Pl. 32. fig. 1) consist of two ovaries (*lo*, *ro*), two oviducts (*od*), a paired valve (*vl*), a spermatheca (*sp*) and spermathecal gland (*spg*), and a common oviduct (*co*) running into the sheaths of the "ovipositor," which terminates in the bursa copulatrix. In addition there is a long flexible cloacal stalk (*lr*) ("Kloakstiel," Stein 11) and two short rods (*sr*).

TEXT-FIG. 2.



A, the ovary of an immature female. B, the ovary of a mature unfertilized female, semi-diagrammatic. *c*, calyx; *ec*, egg-chamber; *et*, ovarian tube; *f*, filament; *tc*, terminal chamber; *re*, ripe eggs. *Camera lucida*,  $\times 54$ .

The ovaries (*lo*, *ro*) of a mature beetle each consist of fourteen ovarian tubes (*et*). Each tube consists of from four to five egg-chambers (*ec*), and a terminal chamber (*tc*) terminating in a filament (*f*). The ovarian tubes arise from an enlargement of the oviducts—the calyx (*c*). The calices act as receptacles for the ripe eggs, which pass into them from the basal egg-chambers. In fig. 1 (Pl. 32) there are three ripe eggs in the left calyx and two in the right.

It was found that the left ovary was always developed earlier than the right.

The ovary of an immature female examined consisted of only ten ovarian tubes (text-fig. 2, A), the other four eventually arising from the apex of the calyx and between the existing tubes. The ovary of a mature unfertilized female (text-fig. 2, B) shows a considerable enlargement of the calyx, which is tightly packed with ripe eggs.

From the calices the eggs pass along short oviducts into a double-chambered valve (*vl*). Each chamber of the valve is lined with brown chitinated setæ\* with their free ends lying in the same direction as that in which the eggs pass (*vl*, Pl. 32. fig. 4). The chambers of the valve meet to form the commencement of the common oviduct, and the setæ terminate some distance before a valvular duct (*vt*) leading into the spermatheca enters the common oviduct.

The spermatheca is very large and terminates in a single tube—the spermathecal or accessory gland. In fertilized females the size of the spermatheca is perceptibly increased. Inside the spermatheca, arising from the ventro-lateral surface at the point (*psp*) where it narrows, are found a series of 27 chitinated setæ (*s*, Pl. 32. fig. 3); their function is obscure. The spermatozoa are mostly in packets—spermatophores (*spp*, Pl. 32. fig. 4),—but a considerable number are found loose in the fluid contents of the spermatheca.

The common oviduct, into which the eggs pass from the valves, is of muscular structure, and finally disappears into the "ovipositor."

The long flexible cloacal stalk (*lr*, Pl. 32. fig. 2) arises from a point in the centre and near the base of the ventral pygidial plate (*rp*). The stalk extends through the middle of the abdomen into the meta-thorax to a point beyond the beginning of the "ovipositor," where its apex enlarges into a knob from which two sets of muscle-fibres ( $m^1$ ,  $m^2$ ) arise. The  $m^1$  set of muscles consists of series of bundles of long fibres grouped around the "ovipositor," and extending from the apex of the cloacal stalk to a point between the short rods (*sr*), where they are attached to the outer sheath (*ots*). The  $m^2$  muscles surround the cloacal stalk to its base, where it is embedded in a mass of muscles. In addition to the muscles ( $m^1$ ,  $m^2$ ), there is another series ( $m^3$ ), which arise around the beginning of the "ovipositor" and completely surround the outer sheath, extending for about half its length, at which point they are attached to it. Further, there are numerous muscle-fibres arising from the same point as the ( $m^3$ ) muscles; these are found longitudinally traversing the inside of the inner sheath (*ins*) of the "ovipositor" (Pl. 34. figs. 4-7). And, in addition, there is a series of cancellate muscles lining the walls of the distal portion of the "ovipositor," apparently

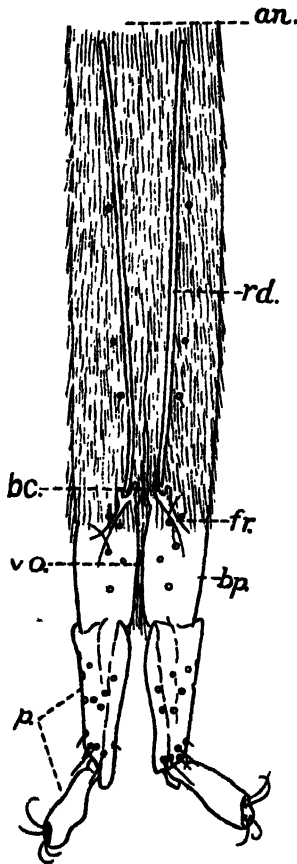
\* In a previous paper, "On the Method of Oviposition and the Egg of *Lyctus brunneus* Steph." (Journ. Linn. Soc., Zool. xxxv. 1923, p. 217), the writer has stated that it is these setæ-lined valves which impart the striations and process to the deposited eggs.

to allow for its expansion during the passage of an egg. Another series of muscles ( $m^4$ ) are found, arising from the lateral walls of the spermatheca and terminating around the common oviduct at a short distance from its base.

The common oviduct enters the "ovipositor" between the  $m^1$  muscles.

When the ovipositor is in repose—as depicted in Pl. 32,—it consists of two sheaths, the outer or basal portion (*ots*), which is a transparent tube lightly chitinized, and the inner sheath or distal portion (*ins*), which is a continuation of the outer sheath. The two portions join at the point where the common oviduct enters. The surface of the distal portion of the "ovipositor"

TEXT-FIG. 3.



Apex of the ovipositor, ventral. *an*, anus; *bc*, bursa copulatrix; *bp*, basal piece; *fr*, forked rod; *p*, vaginal palp; *rd*, chitinized rod; *vo*, vaginal orifice. *Camera lucida*,  $\times 128$ .

is covered with recumbent brown chitinized setæ, which extend as far as the bursa copulatrix (*bc*, text-fig. 3). The apex of the "ovipositor" (text-fig. 3) is stoutly chitinized, and consists of paired rounded basal pieces (*bp*), between which is the vaginal orifice (*vo*). Arising from each of the basal pieces is a



double-jointed vaginal palp (*p*), which bears a number of sensory pits. The inner lateral faces of the palps are concave. Within each basal piece is a short forked rod (*fr*), and articulating between the prongs of the fork and running back some distance is a chitinized rod (*rd*) ("Seitenstuck," Stein 11).

The abdominal nerve-ganglion and commissures are not depicted; the latter were only traced to the venter of the spermatheca and to the valve.

The left top corner of Pl. 32. fig. 1 depicts a portion of the mesenteron (*ms*) terminating in the ileum (*lm*), from which arise six malpighian tubes (*mp*). The ileum, which is lined with chitinized setæ at its junction with the mesenteron, is followed by the colon (*cl*), which leads into the rectum (*r*). The rectum, which is of muscular structure, is visible for a considerable length before it—like the common oviduct—disappears into the "ovipositor." (In this figure the rectum has been pulled across to the left; it should lie looped over the "ovipositor" and enter from the right as in Pl. 33. fig. 2.)

Pl. 34 depicts the "ovipositor" in section. Figs. 4, 5, 6, and 7 are *camera lucida* drawings of transverse sections from an "immature" female. Fig. 4 shows the rectum (*r*) entering the inner sheath (*ins*) of the ovipositor from the right and assuming a position dorsal to the common oviduct (*co*), which enters from under the left. In fig. 5 the rectum (*r*) is now dorsal to the common oviduct (*co*), and both are completely enclosed by the inner sheath or distal portion (*ins*) of the "ovipositor," which in turn is enclosed within the outer sheath (*ots*). In fig. 6 the rectum (*r*) is seen emerging through the dorsal wall of the distal portion of the "ovipositor"; whilst in fig. 7 the rectum and anus (*an*) are now free of the inner sheath, which, at this point, becomes the integumental covering of the apex of the common oviduct (*co*) or bursa copulatrix.

Fig. 8 is a transverse section through the apex of the "ovipositor" of a fertilized female which had begun egg-laying. The section is about the beginning of the vaginal orifice (*vo*); it shows the stout outer lateral wall of the basal pieces (*bp*) and transverse muscles to allow of expansion.

Figs. 1, 2, and 3 are partially reconstructed *camera lucida* drawings of longitudinal sections of the "ovipositor" of a fertilized female that had been ovipositing. Fig. 1 shows the junction (*jo*) of the inner and outer sheaths, and the entry of the common oviduct from underneath to the ventral surface of the inner sheath and the position of the rectum. Fig. 2 is of a median section of the "ovipositor" showing the rectum convoluted (*rc*). Fig. 3 is a section through that part of the "ovipositor" where the rectum (*r*) emerges through the inner sheath.

The relative positions occupied by the genitalia and alimentary tract within the abdomen, meta- and mesothorax are depicted in Pl. 33. figs. 1, 2, and 3. No muscles are shown, as their inclusion would obliterate a large part of these organs. It will be seen that the female possesses an apodeme (*ap*) of a similar structure to that described in the male. The figs. 1 and 3 are based

on reconstructions made from a series of longitudinal sections of a fertilized female, and depict a left and right lateral view respectively, with the uppermost ovary and oviduct removed in each case. Fig. 2 is based on reconstructions made from balsam mounts of cleared specimens and from dissections, and depicts a dorsal view in which the relatively greater length of the rectum (*r*) of the female in comparison with that of the male (Pl. 31. fig. 4, *r*) is made apparent. The ratio is approximately 30 : 1.

Pl. 32. fig. 2 shows in longitudinal section the dorsal (*dp*) and ventral (*vp*) pygidial plates with the apex of the "ovipositor" between, and also part of the 7th sternite (VII), *i. e.* the 5th sternite of systematists.

The functioning of the parts of the ovipositor appear to be as follows:—

In repose (Pl. 32. fig. 1)  $m^1$ ,  $m^2$ , and  $m^4$  muscles are in a state of contraction, whilst  $m^3$  and the longitudinal series within the inner sheath are in a state of expansion. By the contraction of  $m^3$ , the outer sheath commences to collapse, the distal portion to issue from between the pygidial plates and drawing with it the muscular rectum and the common oviduct. By the simultaneous contraction of the muscles within the inner sheath, the outer sheath is caused to evaginate and issue from between the pygidial plates. The outer sheath continues to evaginate and issue until brought in check by  $m^1$  muscles. When fully extruded the "ovipositor" is approximately the length of the female.

The withdrawal of the ovipositor is apparently achieved by the contraction of the expanded  $m^4$  muscles, aided by the muscular common oviduct, which would pull back into its position of repose, bringing the distal portion of the "ovipositor" with it. Simultaneously, the contraction of  $m^1$  muscles would pull back the basal part of the outer sheath, whilst  $m^3$  muscles would draw into position the apical portion of the sheath.

As there are no muscles attached to the ileum, the colon, or the rectum, the resumption of the position of repose for this portion of the alimentary tract must be solely dependent upon the slight contraction of which the muscular rectum is capable—aided by the fixed mesenteron—and any tension that might be exerted by the ramifications of the trachea. That such is apparently the case is shown in Pl. 34. fig. 2. Here the rectum is seen convoluted—a condition that can only be attributed to an imperfect musculature.

Other sections of the same beetle disclosed two other points within the "ovipositor" where the rectum was similarly convoluted. In this condition no beetle could defæcate unless it extended its "ovipositor," and thus straightened the rectum. Whether this is ever done is not known. But as the food of these beetles consists of particles of wood, most of which appears in the frass never to be broken down, it is possible that penetration of the walls of the rectum and of those of the common oviduct may take place. And it seems probable that this defectiveness may be the cause of the death of quite a

number of beetles whose ovaries are found to contain a considerable portion of their complement of eggs. It has been observed that many beetles do expire with the "ovipositor" extruded—partially in the majority of cases.

When the distal portion of the ovipositor is gently pulled out by means of a fine pair of forceps from a freshly chloroformed beetle, the basal portion is seen to extend after the manner of a telescope.

Females have a gland on each side of the seventh abdominal segment correlated to the glands or sacs described in the male; and they are of similar structure. But in the females they do not meet, and from sections they appear to surround the tracheal trunks leading to the seventh abdominal spiracles.

#### COITION.

It has been mentioned that efforts to kill pairs in coition with the organs *in situ* failed to disclose more of the internal sac of the male than is shown in Pl. 31. fig. 2. And from the examination of the cedeagus the internal sac does not appear to be capable of evaginating more than half the length of the median lobe (Sharp & Muir 10).

In coition the beetles are superimposed, and the lateral lobes of the male assume an almost perpendicular position to the surface of the wood. As the beetles are very flat, the apices of the lateral lobes come in contact with the surface of the wood, and, if the female moves, as is frequently the case, the apices of the lateral lobes become bent and covered with particles of dirt and dust\*.

#### NOTES ON THE GENITAL SYSTEM OF *LYCTUS LINEARIS* GOEZE.

An attempt has been made to carry out a comparative examination of the genital system of *L. linearis*. But no living specimens could be procured, and the following remarks are based upon the study of preparations made from the remains of the organs of dead beetles.

Two beetles—both males—were kindly sent by Dr. Hugh Scott, and three other specimens—one female and two males—were found in the pupal chambers in oak sent from Paris by M. P. Lesne. The oak was sent under the impression that it was infested by the larvæ of this species; however, as no beetles emerged within the normal period, it was broken up and no larvæ or pupæ were found.

The dead beetles obtained were first soaked for five days in water to which a few drops of formaldehyde were added. The specimens were then washed in water and dissected. The dissections were treated in the usual manner and mounted in balsam. The resulting preparations were moderately successful.

\* From a control point of view, this is of considerable importance, for the treatment of the surface of the wood with an oleaginous or viscous substance causes the dirt and dust to adhere to such an extent as to jam the cedeagus—the lateral lobes become stuck to the median lobe, the median orifice becomes blocked, and the beetle is, as a result, killed.

One point observed was that the tergites of *linearis* were much more strongly chitinized than in *brunneus*, in which they are very flexible and only faintly discernible.

*The male.*—The œdeagus was found to agree with the description and figures of Sharp and Muir (10), except that the basal margin of the basal piece was found to terminate in front of the point of articulation, but not so far forward as in *brunneus*. Whether the anterior margin of the basal piece clipped around the lateral lobes was not observed, as no sections were made. In other respects it was similar, and gave the impression of being a more robust structure.

Nothing was found of the testes, but the position and appearance of the remains of the vasa deferentia, seminal vesicles, accessory glands, and ejaculatory duct were similar to those of *brunneus*.

The two rods arising from under the ejaculatory duct as in *brunneus*, and the "U"-shaped apodeme and apodemal rods were present.

*The female.*—The similarity of the extruded "ovipositor" as seen in dead females to that of *brunneus* has been referred to by others. From the preparation made, there were observed the setæ-lined valve and what would be the spermatheca and common oviduct. Remains of the ovaries were present, but the number of ovarian tubes could not be distinguished. The ovipositor, in repose, and the apex of the distal portion bore a marked similarity to those of *brunneus*. Further, the cloacal stalk and short rods, and the apodeme and apodemal rods were present.

From the appearance of the "ovipositor" in repose, it seems that the alimentary tract must follow a similar course to that of *brunneus*.

#### OBSERVATIONS ON STEIN'S 'FEMALE REPRODUCTIVE ORGANS IN COLEOPTERA.'

Stein (11), in his work on the genital system of Coleopterous females, describes and illustrates the organs of several species which in some particulars resemble the organs of *brunneus*. But this resemblance is so slight in most that no comparative deductions can be drawn. There are, however, a few points that call for comment.

The "ovipositor" in each of these cases consists of a tube ("Kloakrohr") which in repose telescopes approximately one-half within the other, but each varies in the appearance of the distal portion. In all cases the "ovipositor" is apparently shorter, in comparison to the length of the insect, than that of *brunneus* and *linearis*. The rectum, in each of the species referred to, enters the inner sheath of the "ovipositor" as in *brunneus*. The cloacal stalk is found, but it is not clear what distance within the abdomen it traverses, and in no case is there any indication of the short rods.

In the case of those females that are closely related systematically to the Lyctids, i. e. *Anobium punctatum* De Geer (*pertinax* F., *domesticum* Fourc.,

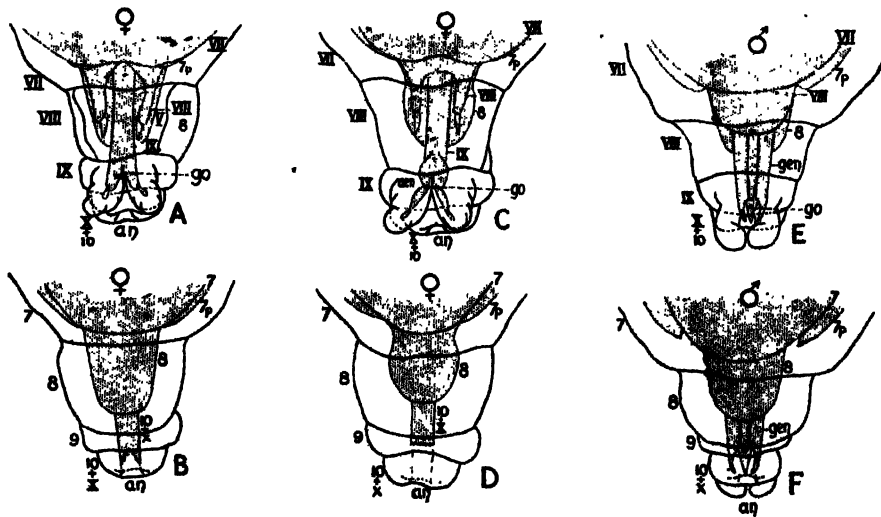
*striatum* Ol.), and *Cis boleti* Scop.\*, the cloacal stalk, according to Stein, is dorsal to the "ovipositor," and it is therefore in a reversed position in *brunneus* and *linearis*. But in the case of other females somewhat distantly related systematically, such as *Helops* (*caraboides* Panz.) *striatus* Fourc., *Edemera* (*virescens*) *lurida* Marsh, and *Cistela fusca*, the cloacal stalk, according to the same authority, lies below the "ovipositor," and, as in *brunneus* and *linearis*, it arises from the venter.

It might also be observed that in *Anobium punctatum* De Geer, Stein describes two accessory glands—in the female, of course. One is unpaired and the other paired, the former lying ventral to the "ovipositor" and the latter pair apparently arising from within the inner sheath of the "ovipositor." Pygidial glands, such as have been found in both sexes of *brunneus*, are not mentioned by Stein.

#### NOTE ON THE MORPHOLOGY OF THE APEX OF THE ABDOMEN IN *LYCTUS BRUNNEUS* STEPH.

This note is based upon a close study of the sections previously referred to, and of a series of balsam mounts of pupæ in various stages of development, as well as various preparations made from the beetles.

TEXT-FIG. 4.



Apex of the abdomen of three pupæ of *L. brunneus* from specimens prepared and mounted in balsam. A, ventral aspect of a female, early stage of development; B, dorsal aspect of the same, seen through the back of the slide. C, ventral aspect of a female, later stage of development; D, dorsal aspect of the same, seen through the back of the slide. E, ventral aspect of a male, late stage of development; F, dorsal aspect of the same, seen through the back of the slide. *an*, anus; *gen*, genitalia; *go*, gonopore; *7p*, seventh pleurite; *7-10*, tergites; *VII-X*, sternites. All figures *camera lucida* outlines,  $\times 66$ .

\* The opportunity to examine specimens of *Cis boleti* Scop. has recently occurred, and the cloacal stalk was found to be ventral to the ovipositor, as in *brunneus*.

Text-fig. 4 depicts the ventral and dorsal aspects of the apex of the abdomen of three pupæ. From these it is apparent that the external appendages of the genitalia in both sexes arise from a similar position, *i.e.* on the ninth sternite (IX) and towards the tenth; the gonopore (*go*) lies medianly between these appendages, and is situated on the ninth sternite.

In the female *L. brunneus* the last visible sternite—the fifth of systematists—is the true seventh sternite (VII) and corresponds with the seventh tergite (7) directly above it (Pl. 33. figs. 1 & 3). The pygidium represents part of the eighth segment with the cloacal stalk (*lr*) an invagination of the eighth sternite (VIII), and the paired rods (*sr*) are lateral invaginations of the eighth tergite (8). This conclusion is supported by the presence of the  $m^1$  and  $m^2$  series of muscles (Pl. 32. fig. 1), which would seem to be modified intersegmental muscles. For the position of attachment of the  $m^1$  set is from the apex of the cloacal stalk to lateral positions near the beginning of the ninth segment—the basal portion of the “ovipositor”; whilst the  $m^2$  set, which envelop the cloacal stalk, arise from the point of its invagination. Moreover, a part of the muscles enveloping the paired rods (*sr*, Pl. 32. fig. 1) are attached laterally to the base of the ninth segment, whilst the remainder of these muscles are attached to the point of invagination of each rod.

The “ovipositor” is, therefore, a double tubular prolongation of the ninth segment, tergites and sternites being indistinguishable. Whether the transparent and setæ-less basal portion of the “ovipositor” represents a prolongation of the “soft membrane” between segments 8 and 9, is not manifest. Intersegmental membrane is not manifest anywhere else. And, conversely, with regard to the setæ-covered distal portion of the “ovipositor,” setæ are not manifest on any tergite but the seventh.

The apex of the ovipositor bears the anus dorsally between the fused and reduced tenth tergite and sternite, and it carries the genitalia on the ninth sternite beyond the anus.

In the male (Pl. 31. figs. 2 & 3) the last visible sternite is the seventh, as in the female; and likewise the pygidium represents the eighth segment. The ninth tergite and sternite are not solidly chitinized, and are invaginated and fused at their beginning to form the lumen enclosing the œdeagus and the anus, the latter being enveloped in a tube (*ev*, fig. 3) formed by the fused tenth tergite and sternite, as in the female. The invaginated ninth segment, the sternal portion of which is invaginated more than the tergal portion, shortly evaginates. Then the tergal portion joins the tergal portion of the tube [*ev* (10), fig. 3]; whilst the sternal portion, in which the gonopore is situated medianly, eventually joins the sternal portion of the tube (X, fig. 2). The ninth sternite is prolonged around the gonopore to form the extrusible membranous tube carrying the œdeagus, to which it is attached, as previously stated, around the basal piece. The paired rods (*vr*, figs. 1 & 3) that project into the abdomen from the tube (*ev*) are invaginations of the

tenth segment, and the three sets of muscles associated with these paired rods are also intersegmental muscles. The lateral sets following the course of the rods represent the muscles of the tenth sternite and tergite, whilst the median set represent those of the tenth and ninth sternite.

The homology between the genitalia of the sexes seems apparent (text-figs. 3 & 4 and Pl. 31. figs. 1 & 3). The sensory-pitted unjointed lateral lobes homologize with the sensory-pitted jointed vaginal palps; the basal pieces correspond; and the evaginated median lobe and extrusible internal sac homologize with the internal forked rods—"seitenstück"—and invaginated uterus. The analogy of their functions is obvious.

In the larva of *L. brunneus* there are nine pairs of spiracles: one prothoracic and eight abdominal pairs. In the adult there are nine pairs of spiracles: one prothoracic, one metathoracic—on the soft integument below the wing-bases—and seven abdominal pairs.

#### SUMMARY.

Both sexes in *L. brunneus* are sexually mature when they have emerged through the wood from their pupal chambers. An external sex-character is described.

In the male the reproductive organs consist of two testes of twelve pyriform testicular follicles of unequal size, six arising from each convoluted vas deferens, which terminate in a pair of jointed subcylindrical seminal vesicles. A short tube arises from each seminal vesicle, and forms the ejaculatory duct which empties into the ædeagus. Partly superimposed over the seminal vesicles and emptying into the short tubes are the paired accessory glands. They are subcylindrical, slightly tapering, and are curved around to underneath the ejaculatory duct. There is a pair of pygidial glands.

In the female the reproductive organs consist of two ovaries, each composed of fourteen ovarian tubes with the nutritive cells situated at their apices. The ripe eggs accumulate in a calyx which continues to form the oviduct. The oviducts terminate in a chitinated setæ-lined paired valve which forms the source of the common oviduct. At this point the voluminous spermatheca arises; it terminates in a tubular spermathecal or accessory gland. The common oviduct disappears into the invaginated double tubular "ovipositor" at a point in the metathorax, where the rectum also enters.

In the testicular follicles the spermatozoa are in bundles, in the spermatheca they are in packets or spermatophores.

The "ovipositor" has been found to consist of a double tubular prolongation of the ninth abdominal segment, with a reduced tenth segment towards the apex. When extruded the "ovipositor" is approximately the length of the beetle. Situated at the apex of the "ovipositor" are the genitalia with the anus a short distance behind.

Arising as an invagination of the eighth sternite and extending into the metathorax is the long, flexible, and strongly-chitinized cloacal stalk, from which arise systems of muscles for exerting and withdrawing the ovipositor. These muscles are found to be modified intersegmental muscles.

Morphologically the gonopore in both sexes was found to arise medianly on the ninth sternite, and the homology of the genitalia appears.

In the larva of *L. brunneus* there are nine pairs of spiracles, one thoracic and eight abdominal; in the adult there are also nine pairs, two thoracic and seven abdominal.

The movement which the rectum of the female is subjected to has been observed to be injurious to this organ, in that, lacking any muscular system for its withdrawal, other than its muscular structure, it was found convoluted inside the "ovipositor" of an egg-laying specimen. This defectiveness must accelerate death.

#### ACKNOWLEDGMENTS.

The economic investigation, of which this paper records part of the results, was suggested by Prof. H. Maxwell-Lefroy, Imperial College of Science, to whom the writer has to express his thanks, and to the Committee of the Scientific Industrial Research Dept. for a grant to carry on the work.

The writer is also indebted to Dr. C. J. Gahan, Keeper of the Department of Entomology, British Museum (Nat. Hist.), for identifying specimens of *L. brunneus*; to Dr. Hugh Scott, Cambridge Museum, for specimens of *L. linearis*; and to M. P. Lesne, Mus. Nat. d'Hist. Nat., Paris, for very kindly sending some oak thought to be infested with *L. linearis*.

In addition, thanks are due to Dr. A. D. Imms, Rothamsted Experimental Station, for his advice and for his assistance in connection with the publication of this paper; and to Prof. Stewart MacDougall for his efforts to have the original paper published as a whole.

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## EXPLANATION OF THE PLATES.

## PLATE 31.

- Fig. 1. Male genitalia. Semi-diagrammatic.  $\times$  circa 51.
- Fig. 2. Transverse section (slightly oblique) through apex of abdomen of immature male.  $\times$  100.
- Fig. 3. Right lateral aspect of apex of male abdomen.  $\times$  114.
- Fig. 4. Diagrammatic ventral aspect of seminal vesicles, accessory glands and their junction with branched ejaculatory duct.  $\times$  circa 51.
- Fig. 5. Diagrammatic dorsal aspect of genitalia and alimentary tract *in situ*. Greatly magnified.

## PLATE 32.

- Fig. 1. Female genitalia (*camera lucida*) and part of alimentary tract (partly diagrammatic).  $\times$  51.
- Fig. 2. Longitudinal section through apex of female's abdomen.  $\times$  384.
- Fig. 3. Transverse section through spermatheca. *C. l.*  $\times$  384.
- Fig. 4. Longitudinal section through base of spermatheca and valves of oviduct. *C. l.*  $\times$  384.

## PLATE 33.

Arrangement *in situ* of genitalia and alimentary tract of female.

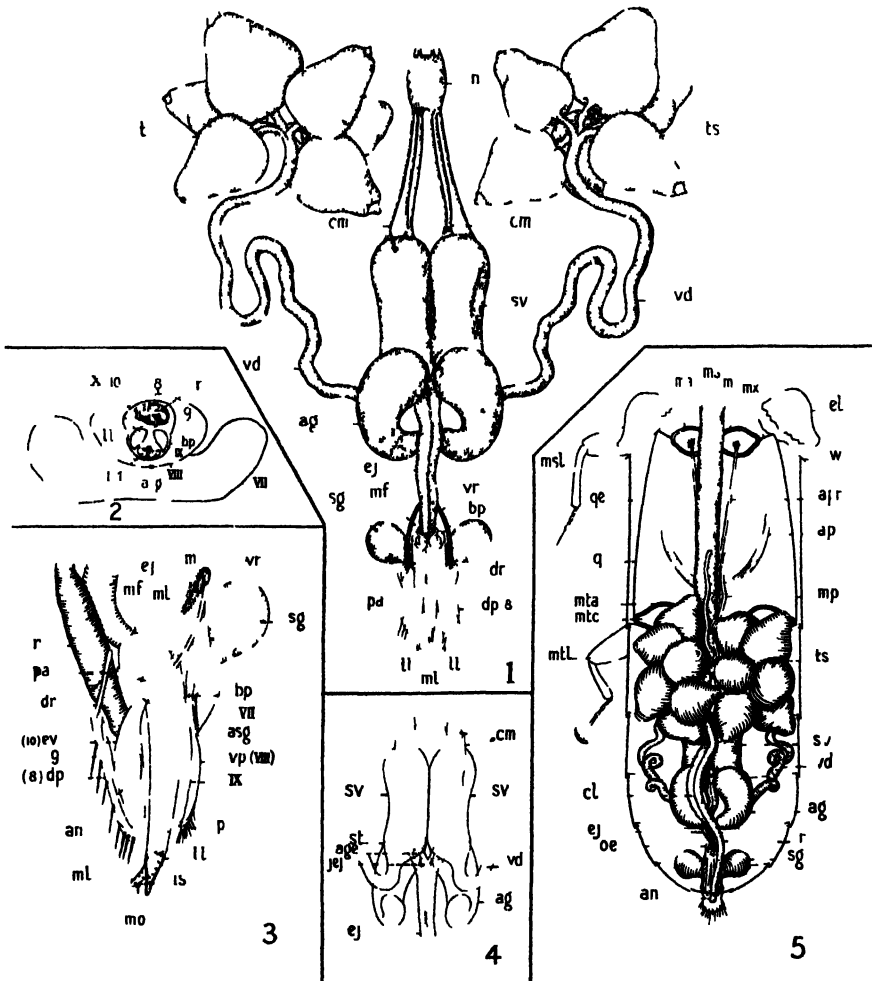
Partly reconstructed from sections and partly diagrammatic. Greatly magnified.

- Fig. 1. Left lateral view. Position of repose.
- Fig. 2. Dorsal view. Position of repose.
- Fig. 3. Right lateral view. Position when ovipositor extruded.

## PLATE 34.

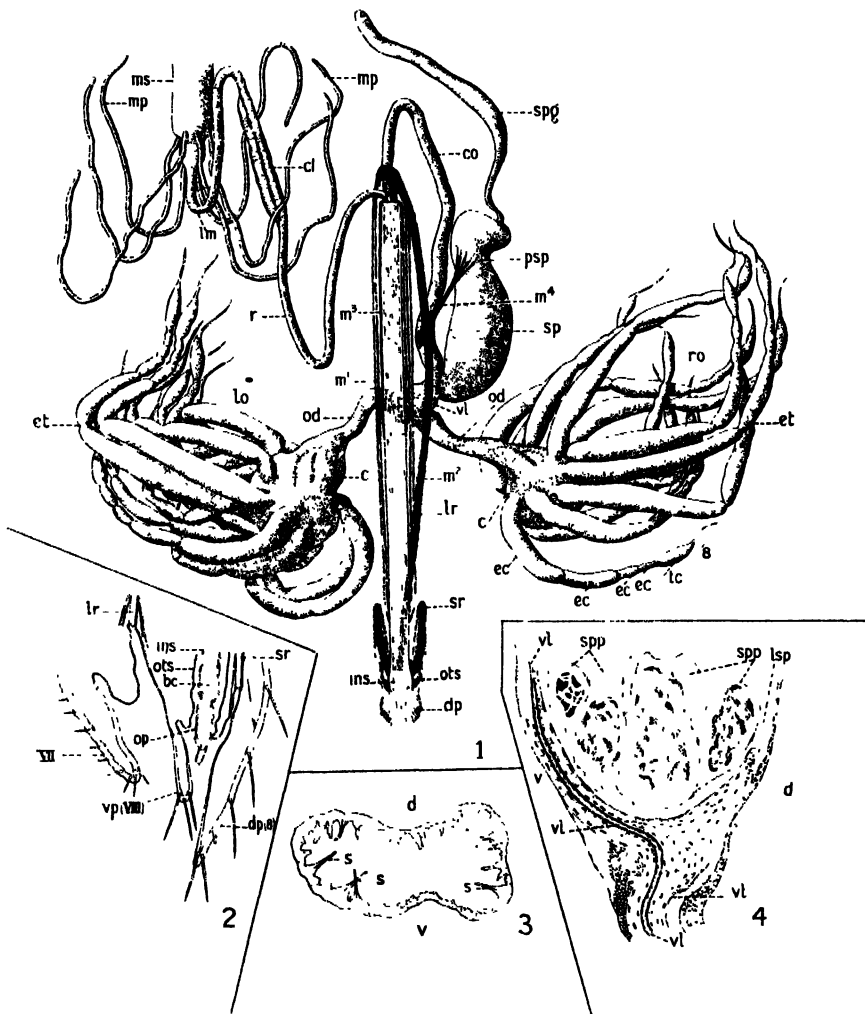
- Fig. 1. Longitudinal section through ovipositor at junction of inner and outer sheaths.
- Fig. 2. Longitudinal section through middle of ovipositor, shewing rectum convoluted.
- Fig. 3. Longitudinal section through ovipositor, showing rectum and common oviduct separating.
- Fig. 4. Transverse section of ovipositor at junction of inner and outer sheaths.
- Fig. 5. Transverse section of middle of ovipositor.
- Fig. 6. Transverse section of ovipositor, showing rectum and common oviduct separating.
- Fig. 7. Transverse section of ovipositor showing anus free, and common oviduct completely enclosed by inner sheath.
- Fig. 8. Transverse section through bursa copulatrix.

(Figs. 1, 2, and 3 are of a mature fertilized female. Part *C. l.* and partly reconstructed, Figs. 4, 5, 6, and 7 are of an immature female, *C. l.* Fig. 8 is of a fertilized female, *C. l.* All figures  $\times$  840.)



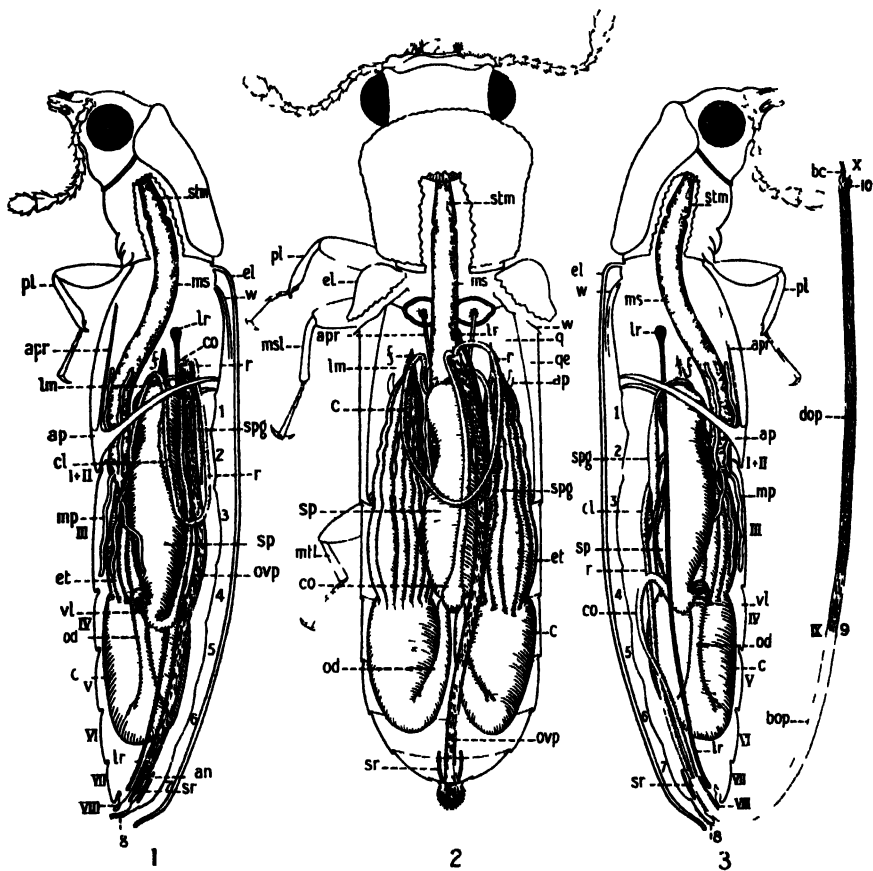
GENITAL SYSTEM OF LYCTUS





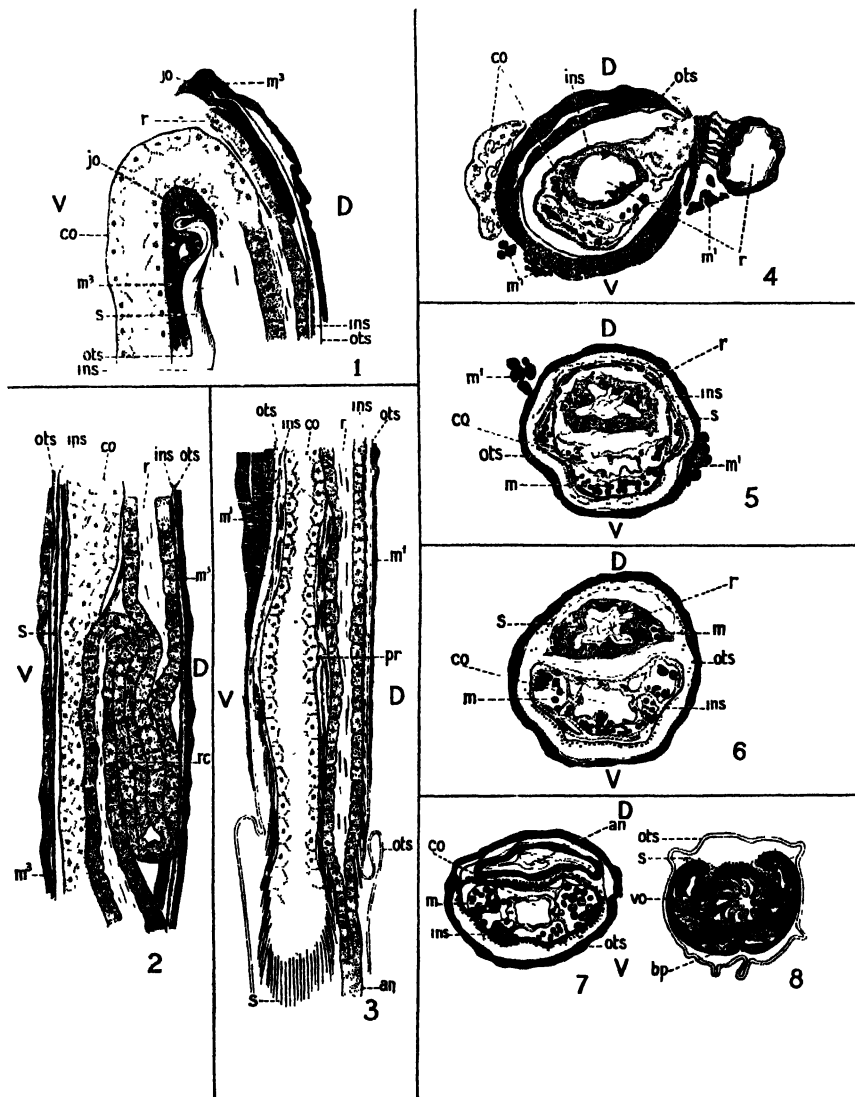
## GENITAL SYSTEM OF LYCTUS.





GENITAL SYSTEM OF LYCTUS.





GENITAL SYSTEM OF LYCTUS.





## REFERENCE LETTERING.

*ag*, accessory gland; *age*, junction of accessory gland and ejaculatory duct; *an*, anus; *asg*, aperture of secreting glands; *ap*, apodeme; *apr*, rod of apodeme; *bc*, bursa copulatrix; *bop*, basal portion of ovipositor; *bp*, basal piece; *c*, calyx; *cl*, colon; *co*, common oviduct; *cm*, commissure; *d*, dorsal; *dop*, distal portion of ovipositor; *dp*, dorsal pygidial plates (8th tergite); *dr*, dorsal rod; *ec*, egg-chambers; *ej*, ejaculatory duct; *el*, elytron; *et*, ovarian tubes; *ev*, enveloping sheath; *f*, filament; *in*, integumental sheath; *ins*, inner sheath of ovipositor; *is*, internal sac; *jef*, junction of ejaculatory duct; *jo*, junction of outer and inner sheaths of ovipositor; *ll*, lateral lobes; *lm*, ileum; *lo*, left ovary; *lr*, cloacal stalk; *lsp*, loose spermatozoa; *m*, muscles; *m<sup>1</sup>-m<sup>4</sup>*, sets of muscles; *ma*, mesothoracic acetabula; *mc*, mesothoracic coxa; *mf*, median foramen; *ml*, median lobe; *mo*, median orifice; *mp*, malpighian tubes; *ms*, mesenteron; *mal*, mesothoracic leg; *mta*, metathoracic acetabula; *mtc*, metathoracic coxa; *mtl*, metathoracic leg; *mx*, suture between meso- and metasternum; *n*, abdominal nerve-ganglion; *ol*, oviduct; *oe*, oedeagus; *op*, 2-jointed vaginal palp of ovipositor; *ots*, outer sheath of ovipositor; *ovp*, ovipositor; *p*, palp; *pa*, point of articulation; *pl*, prothoracic leg; *pr*, point of extrusion of anus; *ppp*, setæ inside spermatheca; *q*, metasternum; *qe*, episternum of metasternum; *r*, rectum; *rc*, convoluted rectum; *ro*, right ovary; *s*, setæ; *sg*, secreting glands; *sp*, spermatheca; *spy*, spermathecal gland; *spp*, packets of spermatozoa (spermatophores); *sr*, short rod; *st*, branch of ejaculatory duct; *stm*, stomodeum; *sv*, seminal vesicle; *tc*, terminal chamber; *ts*, testes; *v*, ventral; *vd*, vas deferens; *vo*, vaginal orifice; *vp*, ventral pygidial plate (VIII sternite); *vr*, ventral rods; *w*, valvular duct; *w*, wing; 1-10 tergites, I-X sternites.



The Foraminifera of Lord Howe Island, South Pacific.  
By E. HERON-ALLEN, F.R.S., F.L.S., and A. EARLAND, F.R.M.S.

(PLATES 35-37.)

[Read 21st June, 1923.]

THE highly interesting material which forms the subject of the present Monograph was collected by Prof. R. Douglas Laurie during the visit of the British Association to Australia in 1914. We may quote his own description, which is as follows:—"It consists of material taken from between tide-mark at 'Middle Beach' on the east side of the Island, which is the exposed side, *i. e.* without a coral reef. There is a little coral to be seen growing on this shore at low tide, but on the other—on the west side of the Island—is a coral reef quite well developed and protecting a lagoon, about a mile from the land.

"Middle Beach, observation spot; Lat.  $31^{\circ} 31' 30''$  S., Long.  $159^{\circ} 15' 28''$  E.

"Lord Howe Island is the most southerly Pacific Island with a coral reef. Norfolk Island, though about  $2^{\circ} 30'$  further north, has none, nor is there one on the Australian Pacific coast at similar latitude.

"The whole of the material was collected from one small beach; from two different levels. 58 *b*, hardened coral sand and weed from rock-pools at lower half of the beach; 58 *c*, loose surface coral sand to an approximate depth of  $\frac{1}{4}$  inch, from three-quarter high-tide line."

Prof. Laurie sent us a preliminary sample, with a view to ascertaining the value of the material, from 58 *c*, and, this having promised excellent results, he subsequently sent us seven bottles, which may be described as follows:—

No. 1. In 70 % alcohol. This had never been dried. (58 *b*.)

" 2 & 3. " " This had been previously dried at  $50^{\circ}$  C. These yielded about 10 cc. of "floatings." Much byssus and organic material. Many species in the finer siftings, and notable specimens of *Nubecularia bradyi*, *N. schauinslandi*, and *Discorbina polystomelloides* in the coarser grades.

" 4. A small bottle containing *Orbitolites* only; ranging from minute specimens up to individuals 6 mm. in diameter. Dried without heat. (58 *b*.)

" 5. Similar material in 70 % alcohol. Never dried. (58 *b*.)

" 6. A single dried specimen of *Orbitolites complanata*, with the monstrous rectangular secondary outgrowth. (From 58 *b*.)

No. 7. The residue of the preliminary sample from 58 *c*, dried without heat. This material was coarse, and yielded practically no "floatings," the Foraminifera being a good deal worn. It consisted largely of *Orbitolites* and *Tinoporus* (*Baculogypsina sphaerulata*) with about twenty other species of robust types, among which *Amphistegina lessonii*, *Textularia agglutinans*, and its ally *Haddonina torresiensis* were prominent.

Perhaps the most notable feature of the gatherings was the presence of two genera new to science, *Diffusilina* and *Cratemitis*, which are fully described and figured in this monograph.

Another very noteworthy and interesting feature was the profuse occurrence of species in the reproductive stages, both by viviparity and "budding." We have called attention, in our notes, to *Nubecularia lucifuga*, *Spirillina campanula* (sp. nov.), *Discorbina tabernacularis*, *Gypsina inhaerens*, and others, containing young brood in the cavity of the test, resulting from the absorption of the internal septa. Beyond this, certain species (e. g., *Bulimina elegantissima*) exhibited unquestionable evidence of the reproduction by "budding" from the aperture, described at length and illustrated by Heron-Allen in the Phil. Trans. of the Royal Society (H-A. 1915, RPF.).

Among the 199 species and varieties described from the material submitted to us, seven are new to science. Perhaps the most noteworthy species, beyond these, are *Nubecularia schauinslandi*, *Miliolina kerimbaticu*, *M. stelligera*, *Fischerina pellucida*, *Iridia diaphana*, *Haddonina torresiensis*, *Ehrhardiella scottii*, *Uvigerina selseyensis*, *Ramulina grimaldii*, and *Discorbina reniformis*.

We may be allowed to say that we have never had material submitted to us which has been more carefully collected and preserved for examination. Our only regret is that it should have been collected from reefless areas only. No complete study of the foraminiferal fauna of the Island can be made under such reservation. The material shows that a large proportion of the specimens are not of local origin, but are more or less water-worn shells which have travelled some distance. The more perfect specimens, of local origin, are, in the case of a number of species, rather small and pauperate, probably evidencing existence under difficulties, due, no doubt, to paucity of food on the exposed side of the Island. A collection made on the eastern side of the Island, among the reefs and in the still waters of the Lagoon, would probably have yielded a much longer list.

The general facies of the foraminiferal fauna is, of course, sub-tropical and of the Indo-Polynesian type. Many of the species recorded have a wide range, from East Africa, through the Malay and Australasian Seas, to the Pacific. Perhaps the most significant feature is the marked rarity of certain genera which might reasonably have been expected to occur in abundance, e. g., *Hauerina*, *Peneroplis*, *Alveolina*, *Polytrema*, *Opérculina*, *Heterostegina*, and so on, and the entire absence of many typical species which we should have expected to find in such latitudes and in such conditions.

Sub-Kingdom **PROTOZOA.**Class **RHIZOPODA.**Order **FORAMINIFERA.**Family **MILIOLIDÆ.**Sub-family **NUBECULARIINÆ.****NUBECULARIA** *DeFrance.*1. **NUBECULARIA LUCIFUGA** *DeFrance.* (Pl. 35. fig. 1.)

*Nubecularia lucifuga* DeFrance, 1825, Dict. Sci. Nat. vol. xxxv. p. 210; Atlas Zooph. pl. 14. fig. 3.

„ „ Brady, 1884, FC. p. 134, pl. 1. figs. 9-16.

„ „ Cushman, 1910, etc., FNP. 1917, p. 41, pl. 8. fig. 6.

Frequent, but not very typical, displaying a tendency to run into straight lines of chambers. In one specimen the broken final chamber shows what is apparently a young individual fitting closely into the conformation of the chamber. The young specimen consists of four inflated chamberlets arranged on a rotuline plan. The surface appears to be pitted, but not perforate. Texture very thin and delicate.

2. **NUBECULARIA BRADYI** *Millett.*

*Nubecularia inflata* Brady, 1884, FC. p. 135, pl. 1. figs. 5-8.

„ *bradyi* (nom. nov.) Millett, 1898, etc., FM. 1898, p. 261, pl. 5. fig. 6.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 550, pl. 40. figs. 8-10.

Abundant and very variable.

3. **NUBECULARIA SCHAUMSLANDI** (*Rhumbler*). (Pl. 35. figs. 2-5.)

*Miliolina schaumslandi* Rhumbler, 1906, FLC. p. 41, pl. 3. figs. 20, 21.

*Quinqueloculina* „ Cushman, 1910, etc., FNP. 1917, p. 56, pl. 8. figs. 7, 8 (after Rhumbler).

Frequent and very variable. The test, so far as external appearances go, starts with a perfectly normal and well-developed individual comparable with *Miliolina rotunda* or *M. labiosa*, followed by a straight or curving series of irregularly formed chambers terminating in a large, gaping, irregular orifice, narrowed down by a variable number of projecting teeth. It appears to be nothing more than a strongly-developed *Nubecularia bradyi*, and is certainly much more closely allied to that form than to the milioline series of the initial chambers. The more regularly shaped specimens suggest *Nevillina coronata* (Millett), but are very different from Sidebottom's specimens (Manchester Mem. vol. xlix. 1905, No. 11), the types of which are

in our collection. The points of difference lie in the extremely regular disposition of the chambers in *Nevillina*, and particularly in the distinctive crown-like aperture. Millett's original type-specimen of *Biloculina coronata*, which is also in our collection, is, on the contrary, much more likely to be referable to *Nubecularia schauinslandi* than to *Nevillina coronata*, its only point of identity with *Nevillina* being the fact that the projecting teeth round the aperture actually meet and coalesce instead of remaining distinct and separate as in *Nubecularia schauinslandi*. Otherwise the whole structure and appearance of the specimen is distinctly nubecularine and has no feature in common with *Nevillina coronata*.

### Sub-family MILIOLININÆ.

#### BILOCULINA d'Orbigny.

##### 4. BILOCULINA RINGENS, var. STRIOLATA Brady.

*Biloculina ringens*, var. *striolata* Brady, 1884, FC. p. 143, pl. 3. figs. 7, 8.

" " " Millett, 1898, etc., FM. 1898, p. 262, pl. 5. fig. 8.

" " " Heron-Allen & Earland, 1914-15, FKA. p. 551.

Rare. The specimens agree entirely with Brady's description and figure.

##### 5. BILOCULINA SARSI Schlumberger.

*Biloculina sarsi* Schlumberger, 1891, BGF. p. 166, pl. 9. figs. 55-59, text-figs. 10-12.

" " Cushman, 1921, FP. p. 471, pl. 97. fig. 1, text-fig. 48.

Rare. The specimens are fairly large and distinctive.

##### 6. BILOCULINA DEPRESSA d'Orbigny.

*Biloculina depressa* d'Orbigny, 1826, TMC. p. 298, no. 7; Modèle, no. 91.

" " Brady, 1884, FC. p. 145, pl. 2. figs. 12, 15-17; pl. 3. figs. 1, 2.

Very rare.

##### 7. BILOCULINA DEPRESSA, var. SERRATA Bailey.

*Biloculina depressa*, var. *serrata* Bailey, 1861, New Spp. Micr. Org. Para River, S. America. Boston Journ. Nat. Hist. vol. vii. p. 350, pl. 8. fig. E.

" " " Cushman, 1910, etc., FNP. 1917, p. 75, pl. 29. fig. 2.

A single specimen, the serration being confined to the aboral half of the shell.

8. *BILOCULINA ELONGATA* d'Orbigny.*Biloculina elongata* d'Orbigny, 1826, TMC. p. 298, no. 4.

" " Brady, 1884, FC. p. 144, pl. 2. fig. 9.

" " Heron-Allen &amp; Earland, 1913, CI. p. 22, pl. 1. fig. 4.

Very rare, but fairly typical.

9. *BILOCULINA OPPOSITA* Deshayes.*Biloculina opposita* Deshayes, 1831, COT. p. 252, pl. 3. figs. 8-10.

" " Brown, 1837, LG. p. 1143, pl. 42. fig. 30.

(Encycl. Méthodique, vol. ii. p. 138, *sic* Brown.)" *oblonga* d'Orbigny, 1839, FC. p. 163, pl. 8. figs. 21-23.

Three small but distinctive specimens which agree remarkably well with Deshayes' figures, except as regards the tooth, which is not strongly furcate as in his specimens, but less prominent as in d'Orbigny's *B. oblonga*, which is, in other respects, identical with Deshayes' earlier figure. This form may be regarded as an abbreviated and inflated variety of *B. elongata*.

*SPIROLOCULINA* d'Orbigny.10. *SPIROLOCULINA ANTILLARUM* d'Orbigny.*Spiroloculina antillarum* d'Orbigny, 1839, FC. p. 166, pl. 9. figs. 3, 4.

" " Brady, 1884, FC. p. 155, pl. 10. fig. 21.

" " Heron-Allen &amp; Earland, 1908, etc., SB. 1911, p. 301.

Abundant. One of the most typical forms in the gathering. The final pair of chambers is usually so turgid as almost to enclose all the preceding chambers.

11. *SPIROLOCULINA CANALICULATA* d'Orbigny.*Spiroloculina canaliculata* d'Orbigny, 1846, FFV. p. 269, pl. 16. figs. 10-12." " Jones, Parker, & Brady, 1866, etc., MCF. p. 16  
pl. 3. figs. 39, 40.

" " Cushman, 1921, FP. p. 395, pl. 80. fig. 3.

Very rare and weak, and exhibiting a tendency to separation of the chambers, so as to leave lacunae between the adjacent chambers, as in *S. acutimargo* Brady.

12. *SPIROLOCULINA PLANULATA* (Lamarck).*Miliolites planulata* Lamarck, 1804, AM. p. 352, no. 4.*Spiroloculina* " Brady, 1884, FC. p. 148, pl. 9. fig. 11.

" " Heron-Allen &amp; Earland, 1914-15, FKA. p. 555.

A single large specimen which on one side is plane and on the other feebly costate, a variation referred to in FKA. (*ut supra*).



13. *SPIROLOCULINA TENUIROSTRA* Karrer. (Pl. 35. figs. 6, 7.)*Spiroloculina tenuirostra* Karrer, 1867, FO. p. 358, pl. 2. fig. 5.,, *acutimargo* Brady, 1884, FC. p. 154, pl. 10. fig. 14 (only).

,, ,, Egger, 1893, FG. p. 222, pl. 1. figs. 26-28.

A single specimen, identical with Egger's figure of *S. acutimargo* Brady. Under this name Brady figures three distinctive forms. Fig. 12 is clearly *S. affixa* Terquem. Figs. 13 and 15 are what we may regard as *S. acutimargo* proper. Fig. 14 is a quite distinctive little shell which Cushman (C. 1921, FP. p. 398), under *S. acutimargo*, attributes to the genus *Massilina*. It is the same as Egger's figure and is in our opinion attributable to *S. tenuirostra* Karrer, the distinctive features of which are a sharp angular edge to the thin embracing chambers, almost meeting over the faces of the shell. In our specimen the embracing character is so marked that the two final chambers with their flanges envelop the entire face, and the separate chambers are only visible where the surface of the test is abraded. We have observed this form in many tropical coral sands.

## MILIOLINA Williamson.

14. *MILIOLINA CIRCULARIS* (Bornemann).*Triloculina circularis* Bornemann, 1855, FSH. p. 349, pl. 19. fig. 4.*Miliolina* ,, Brady, 1884, FC. p. 169, pl. 4. fig. 3; pl. v. figs. 13, 14 (?).

,, ,, Heron-Allen &amp; Earland, 1914-15, FKA. p. 557.

Abundant, and very variable in size. Both biloculine and triloculine forms, as figured by Millett (M. 1898, etc., FM. 1898, p. 499, pl. 11. figs. 1-3), the biloculine being relatively rare.

15. *MILIOLINA VALVULARIS* (Reuss).*Triloculina valvularis* Reuss, 1851, FSUB. p. 85, pl. 7. fig. 56.*Miliolina* ,, Brady, 1884, FC. p. 161, pl. 4. figs. 4, 5.

,, ,, Heron-Allen &amp; Earland, 1913, CI. p. 27.

Fairly frequent, but small.

16. *MILIOLINA DILATATA* (d'Orbigny).*Quinqueloculina dilatata* d'Orbigny, 1839, FC. p. 192, pl. 11. figs. 28-30.,, ,, Schlumberger, 1893, MGM. p. 75, text-figs. 29, 30,  
pl. 3. figs. 70-74; pl. 4. figs. 87-90.*Miliolina* ,, Heron-Allen & Earland, 1914-15, FKA. p. 559.

Two large characteristic individuals.

17. *MILIOLINA LABIOSA* (d'Orbigny).*Triloculina labiosa* d'Orbigny, 1839, FC. p. 178, pl. 10. figs. 12-14.*Miliolina* ,, Brady, 1884, FC. p. 170, pl. 6. figs. 3-5.

,, ,, Millett, 1898, etc., FM. 1898, p. 502, pl. 11. figs. 8, 9.

Rare, but typical.

18. *MILIOLINA SUBROTUNDA* (Montagu).*Vermiculum subrotundum* Montagu, 1803, TB. pt. 2, p. 521.*Miliolina subrotunda* Brady, 1884, FC. p. 168, pl. 5. figs. 10, 11.

Frequent and small.

19. *MILIOLINA SEMINUDA* (Reuss).*Quinqueloculina seminuda* Reuss, 1866, FABS. p. 125, pl. 1. fig. 11.*Miliolina subrotunda* (Montagu), var., Wright, 1885-6, BLP. p. 319, p. 26. fig. 5.,, *seminuda* Heron-Allen & Earland, 1914-15, FKA. p. 560.

Not uncommon, variable in the number of striæ, which tend to spread over the entire surface of the shell, thus linking the species with *M. webbiana* (d'Orb.).

20. *MILIOLINA WEBBIANA* (d'Orbigny).*Triloculina webbiana* d'Orbigny, 1839, FIC. p. 140. pl. 3. figs. 13-15.*Miliolina fichteliana* Brady, 1884, FC. p. 169, pl. 4. fig. 9.,, *suborbicularis* Millett, 1898, etc., FM. 1898, p. 502, pl. 11. fig. 13.,, *webbiana* Heron-Allen & Earland, 1914-15, FKA. p. 560.

Rare.

21. *MILIOLINA TRIGONULA* (Lamarck).*Miliolites trigonula* Lamarck, 1804, AM. vol. v. p. 351, no. 3.*Triloculina* ,, d'Orbigny, 1826, TMC. p. 299, pl. 16, figs. 5-9; Modèle, no. 93.*Miliolina* ,, Brady, 1884, FC. p. 164, pl. 3. figs. 14-16.

Frequent. All the specimens are of the very elongate type, comparable with *M. affinis* (d'Orb.) (F. 1905, SOM. p. 59, pl. 1. fig. 2).

22. *MILIOLINA TRICARINATA* (d'Orbigny).*Triloculina tricarinata* d'Orbigny, 1826, TMC. p. 299. no 7; Modèle, no. 94.*Miliolina* ,, Brady, 1884, FC. p. 165, pl. 3. fig. 17.*Triloculina* ,, Cushman, 1921, FP. p. 454, figs. 35, 36.

Rare. Both long and short forms occur.

23. *MILIOLINA BERTHELINIANA* Brady.*Miliolina bertheliniana* Brady, 1884, FC. p. 166, pl. 114. fig. 2.

,, ,, Heron-Allen &amp; Earland, 1914-15, FKA. p. 563, pl. 41. figs. 32-35.

Very rare. Both long and short forms occur.

24. *MILIOLINA CULTRATA* Brady.*Miliolina cultrata* Brady, 1879, etc., ERC. 1881, p. 45.

,, ,, Brady, 1884, FC. 161, pl. 5. figs. 1, 2.

,, ,, Heron-Allen &amp; Earland, 1914-15, FKA. p. 564, pl. 42. figs. 1-10.

A single very long and delicate individual.

25. *MILIOLINA BOSCIANA* (*d'Orbigny*).

*Quinqueloculina bosci* d'Orbigny, 1839, FC. p. 191, pl. 11. figs. 22-24.

*Miliolina* „ Millett, 1898, etc., FM. 1898, p. 267, pl. 6. fig. 1.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 566.

Small, but not uncommon.

26. *MILIOLINA OBLONGA* (*Montagu*).

*Vermiculium oblongum* Montagu, 1803, TB. p. 522, pl. 14. fig. 9.

*Miliolina oblonga* Brady, 1884, FC. p. 160, pl. 5. fig. 4.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 566.

Not uncommon. Both the square and the rounded types occur, the rounded predominating. One of the latter is characterized by a long stopper-like tooth, such as we noted from Clare Island (H.-A. & E. 1913, (11. p. 25).

27. *MILIOLINA ROTUNDA* (*d'Orbigny*).

*Triloculina rotunda* d'Orbigny, 1826, TMC. p. 299, no. 4.

*Miliolina* „ Millett, 1898, etc., FM. 1898, p. 267, pl. 5. figs. 15, 16.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 568, pl. 42.  
figs. 27-30.

Two distinct forms occur, one moderately frequent of the triloculine type figured by Millett (*ut supra*), the other of the distinctive d'Orbignyan type, large, thick-shelled, and finely striate.

28. *MILIOLINA VULGARIS* (*d'Orbigny*).

*Quinqueloculina vulgaris* d'Orbigny, 1826, TMC. p. 302, no. 33.

„ „ Schlumberger, 1893, MGM. p. 65, pl. 2. figs. 65, 66.  
& woodcuts 13, 14.

*Miliolina vulgaris* Heron-Allen & Earland, 1914-15, FKA. p. 569.

Large, typical, and frequent.

29. *MILIOLINA SEMINULUM* (*Linné*).

*Serpula seminulum* Linné, 1767, SN. p. 1264, no. 791.

*Miliolina* „ Brady, 1884, FC. p. 157, pl. 5. fig. 6.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 569.

Common. Varying greatly in size and occasionally reaching very large dimensions.

30. *MILIOLINA (TRILOCULINA) LÆVIGATA* (*d'Orbigny*).

*Triloculina lævigata* d'Orbigny, 1826, TMC. p. 300, no. 15.

„ „ Terquem, 1878, FEP. p. 57, pl. 5. (10) figs. 20-21.

„ „ Schlumberger, 1893, MGM. p. 205, pl. 1. figs. 45-47.

„ „ Heron-Allen & Earland, 1922, FGA. pl. 1. figs. 11-14.

Two quite typical specimens. The surface-texture is rather rough.

**31. MILIOLINA TRIANGULARIS (d'Orbigny).**

*Quinqueloculina triangularis* d'Orbigny, 1826, TMC. p. 302, no. 34; 1846, FFV. p. 288, pl. 18. figs. 7-9.

*Miliolina* „ Jones, Parker, & Brady, 1860, etc., MFC. 1895, p. 118. pl. 4. fig. 1, and pl. 6. figs. 2, a-b.

Typical specimens. Rare.

**32. MILIOLINA AUBERIANA (d'Orbigny).**

*Quinqueloculina auberiana* d'Orbigny, 1839, FC. p. 193, pl. 12. figs. 1-3.

*Miliolina* „ Brady, 1884, FC. p. 162, pl. 5. figs. 8, 9.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 571.

Common and generally small. Large and typical specimens are rare.

**33. MILIOLINA AUBERIANA, var. SEMIRETICULATA, nov. (Pl. 35. figs. 8-10.)**

Having the characteristic form of *M. auberiana*, but with the peripheral margins of the chambers reticulated. (Cushman's *M. kerimbatica*, var. *philippinensis* (C. 1921, FP. p. 438, pl. 89. figs. 2, 3) is a similar form, but the periphery and median wing are rounded instead of sharp as in *M. auberiana*.)

**34. MILIOLINA CUVIERIANA (d'Orbigny).**

*Quinqueloculina cuvieriana* d'Orbigny, 1839, FC. p. 190, pl. 11. figs. 19-21.

*Miliolina* „ Brady, 1884, FC. p. 162, pl. 5. fig. 12.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 571, pl. 42. figs. 33-36.

One weak specimen.

**35. MILIOLINA BICOSTATA (d'Orbigny).**

*Quinqueloculina bicostata* d'Orbigny, 1839, FC. p. 195, pl. 12. figs. 8-10.

*Miliolina bicostata* Goës, 1894, ASF. p. 112, pl. 20. fig. 855.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 572, pl. 42. figs. 42-45.

Large and well-developed and fairly frequent. The specimens differ from the Kerimba individuals in the aperture, which is normal, round, and furnished with the usual tooth, agreeing in these respects with the figure of Goës.

**36. MILIOLINA UNDOSA (Karrer).**

*Quinqueloculina undosa* Karrer, 1867, FO. p. 361, pl. 3. fig. 3.

*Miliolina undosa* Brady, 1884, FC. p. 176, pl. 6. figs. 6-8.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 572, pl. 43. figs. 1-4.

Frequent and typical.

**37. MILIOLINA UNDULATA (d'Orbigny).**

*Quinqueloculina undulata* d'Orbigny, 1826, TMC. p. 302, no. 27.

„ „ Schlumberger, 1893, MGM. p. 71, pl. 1. figs. 53, 54; pl. 2. figs. 60, 61; text-figs. 23, 24.

*Miliolina undulata* Heron-Allen & Earland, 1914-15, FKA. p. 573, pl. 43.  
figs. 5-8.

Very rare and rather small, but quite typical.

38. *MILIOLINA RETICULATA* (*d'Orbigny*).

*Triloculina reticulata* d'Orbigny, 1826, TMC. p. 299, no. 9.

*Miliolina* " Brady, 1884, FC. p. 177, pl. 9. figs. 2-4.

" " Heron-Allen & Earland, 1914-15, FKA. p. 573, pl. 43.  
figs. 9, 10.

Frequent and large, of the quinqueloculine rounded type, with coarse markings.

39. *MILIOLINA PARKERI* *Brady*.

"Quinqueloculina with oblique ridges," Parker, 1858, MIS. p. 53, pl. 5. fig. 10.

*Miliolina parkeri* Brady, 1884, FC. p. 177, pl. 7. fig. 14.

" " Heron-Allen & Earland, 1914-15, FKA. p. 574, pl. 43.  
figs. 11, 12.

Very rare, but large and typical specimens.

40. *MILIOLINA KERIMBATICA* *Heron-Allen & Earland*.

*Miliolina kerimbatica* Heron-Allen & Earland, 1914-15, FKA. p. 575, pl. 43.  
figs. 13-23.

*Quinqueloculina* " Cushman, 1921, FP. p. 437.

A single large and typical individual.

41. *MILIOLINA FUSCA* *Brady*.

*Quinqueloculina fusca* Brady, 1870, FTR. p. 286, pl. 11. fig. 2.

" " Schulze, 1874, etc., R. 1875, p. 134, pl. 6. figs. 19, 20.

*Miliolina* " Heron-Allen & Earland, 1914-15, FKA. p. 576.

Rare, but large and well-developed.

42. *MILIOLINA CONTORTA* (*d'Orbigny*).

*Quinqueloculina contorta* d'Orbigny, 1846, FFV. p. 298, pl. 20. figs. 4-6.

*Miliolina* " Goës, 1894, ASF. p. 111, pl. 20. figs. 851, 852.

" " Cushman, 1921, FP. p. 432, pl. 90. fig. 1.

Frequent and large.

43. *MILIOLINA FERUSSACHI* (*d'Orbigny*).

*Quinqueloculina ferussacii* d'Orbigny, 1826, TMC. p. 301, no. 18; Modèle,  
no. 32.

*Miliolina* " Brady, 1884, FC. p. 175, pl. 113. fig. 17.

" " Heron-Allen & Earland, 1914-15, FKA. p. 578.

Frequent, and all of the feeble smooth type figured by Millett (M. 1898, etc., FM. 1898, p. 508, pl. 12, fig. 7 [fig. 6 in text]).

44. *MILIOLINA LINNÆANA* (d'Orbigny).*Triloculina linneiana* d'Orbigny, 1839, FC. p. 172, pl. 9. figs. 11-13.*Miliolina linneana* Brady, 1884, FC. p. 174, pl. 6. figs. 15-20.

,, ,, Heron-Allen &amp; Earland, 1914-15, FKA. p. 579.

A few very large and typical specimens.

45. *MILIOLINA STRIATA* (d'Orbigny).*Quinqueloculina striata* d'Orbigny, 1836, TMC. p. 301, no. 4.

,, ,, Terquem, 1882, FEP. p. 184, pl. 20. (28) figs. 10-12.

*Miliolina* ,, Heron-Allen & Earland, 1914-15, FKA. p. 579, pl. 44.  
figs. 13-17.

Rare; very small and weak.

46. *MILIOLINA STELLIGERA* (Schlumberger).*Quinqueloculina stelligera* Schlumberger, 1893, MGM. p. 68, pl. 2. figs. 58, 59.*Miliolina* ,, Heron-Allen & Earland, 1913, CI. p. 31, pl. 1.  
figs. 14, 15; 1916, FWS. p. 215, pl. 39, figs. 28-31.

Rare, but typical.

## Sub-family HAUERININÆ.

*HAUERINA* d'Orbigny.47. *HAUERINA COMPRESSA* d'Orbigny.*Hauerina compressa* d'Orbigny, 1846, FFV. p. 119, pl. 5. figs. 25-27.

,, ,, Brady, FC. p. 190, pl. 11. figs. 12, 13.

,, ,, Heron-Allen &amp; Earland, 1914-15, FKA. p. 588.

A single undoubted specimen.

48. *HAUERINA ORNATISSIMA* (Karrer).*Quinqueloculina ornatissima* Karrer, 1868, MFKB. p. 151, pl. 3. fig. 2.*Hauerina* ,, Brady, 1884, FC. p. 192, pl. 7. figs. 15-22.

,, ,, Heron-Allen &amp; Earland, 1914-15, FKA. p. 590.

Two rather poor specimens, not developed to the outspreading stage.

*PLANISPIRINA Seguenza.*49. *PLANISPIRINA AURICULATA* Egger.*Planispirina auriculata* Egger, 1893, FG. p. 245, pl. 3. figs. 13-15.,, ,, Heron-Allen & Earland, 1914-15, FKA. p. 590,  
pl. 46. figs. 3-7.Rare, but the two forms differing in relative length and breadth occur,  
as described in our Kerimba Monograph (*ut supra*).

## Sub-family FISCHERININÆ.

FISCHERINA *Terquem*.50. FISCHERINA PELLUCIDA *Millett*.

*Fischerina pellucida* Millett, 1898, etc., FM. 1898, p. 611, pl. 13. figs. 14, 15.

" " Heron-Allen & Earland, 1914-15, FKA. p. 591.

One excellent and typical specimen.

## Sub-family PENEROPLIDINÆ.

CORNUSPIRA *Schultze*.51. CORNUSPIRA INVOLVENS *Reuss*.

*Operculina involvens* Reuss, 1849-50, FOT. p. 370, pl. 1. (46) fig. 20 (not 30).

(*Cornuspira*, 1861; Model, no 15.)

*Cornuspira* " [Brady, 1884, FC. p. 200, pl. 11. figs. 1-3.

" " Heron-Allen & Earland, 1914-15, FKA. p. 593.

Minute, but not infrequent. Both megalos- and microspheric forms, the first predominating as usual.

52. CORNUSPIRA SELSEYENSIS *Heron-Allen & Earland*.

*Cornuspira* ? Earland, 1905, FBS. p. 199, pl. 13. figs. 2-4.

*Cornuspira selseyensis* Heron-Allen & Earland, 1908, etc., SB. 1909, p. 319, pl. 15. figs. 9-11.

Small and rare.

PENEROPLIS *Montfort*.53. PENEROPLIS PERTUSUS (*Forskål*).

*Nautilus pertusus* Forskål, 1775, Descriptio animalium, p. 125, no. 65.

*Peneroplis* " Brady, 1884, FC. p. 204, pl. 13. figs. 16, 17.

" " Heron-Allen & Earland, 1914-15, FKA. p. 601.

Very rare and extremely pauperate in structure.

54. PENEROPLIS CARINATUS *d'Orbigny*.

*Peneroplis carinatus* d'Orbigny, 1839, FAM. p. 33, pl. 3. figs. 7, 8.

" " Brady, 1884, FC. p. 205, pl. 13. fig. 14.

" " Heron-Allen & Earland, 1914-15, FKA. p. 602.

Also rare, but less pauperate than the *pertusus* type.

ORBITOLITES *Lamarck*.55. ORBITOLITES DUPLEX *Carpenter*.

*Orbitolites duplex* Carpenter, 1856, etc., RF. 1856, p. 220, pl. 5. fig. 10; pl. 9. fig. 10.

" " Brady, 1884, FC. p. 216, pl. 16. fig. 7.

" " Heron-Allen & Earland, 1914-15, FKA. p. 605.

Comparatively infrequent as compared with *O. complanata*. A few specimens exhibit a crumpled development of the marginal rows of chambers, approaching the structure of *Orbitolites complanatus* (*Marginopora vertebralis*), var. *plicata* Dana (1846, in Wilkes's U.S. Exploring Exp. vol. vii. p. 706, pl. 60. fig. 9), which is better known under Brady's varietal name, var. *laciniata*, but there is no indication that these specimens represent a reproductive process as in Dana's variety.

56. *ORBITOLITES COMPLANATA* Lamarck.

*Orbitolites complanata* Lamarck, 1802, Syst. Anim. sans Vert. p. 376.

" " Brady, 1884, FC. p. 218, pl. 16. figs. 1-6; pl. 17 figs. 1-6.

" " Heron-Allen & Earland, 1914-15, FKA. p. 606.

Extremely common, but never reaching any great dimensions. No specimens of var. *plicata* or viviparous individuals were observed.

*CRATERITES* Heron-Allen & Earland.

*CRATERITES*, gen. nov.

This new genus is founded for the reception of a single specimen, which, while evidently closely connected with *Orbitolites*, cannot by any stretch of generic definition be included with hitherto recorded types. The closest search through the material available has not resulted in the discovery of other specimens or of anything which might be regarded as an earlier or more advanced condition of growth, and we feel compelled, against our usual practice, on such very insufficient data, to institute a new genus for what is unquestionably a novel and interesting type of construction. Future research may render it necessary to amplify or amend our description, or may possibly relegate the specimen to the position of a freak or a pathological development of *Orbitolites complanatus*.

57. *CRATERITES RECTUS*, sp. nov. (Pl. 35. figs. 11, 12.)

The type-specimen is free, but the base, which is roughly quadrilateral in form, suggests that it was once sessile on some other object. The basal layer consists of a nubecularine mass of chambers without a trace of spiral disposition. Arising from this outspread basal layer is a thick trunk nearly circular in section, composed of five or six superimposed rings of chamberlets, orbitoline in appearance, but devoid of marginal pores. From this point the trunk rapidly increases to nearly double its diameter at its narrowest point by the addition of further superimposed rings of orbitoline chambers without marginal pores. The greatest diameter of the test is reached at a point which is about twelve layers of chambers above the rim of the base. From this widest point the upper surface of the test is completed by a thin and highly convex cover, which bears no trace of septation, but is entirely covered with



coarse perforations, like the rose of a watering-can. Where this oral layer, which closely resembles the marginal edge of *Orbitolites complanata*, has been broken away at a point on the edge, a similar cribrate septum is visible underneath.

The specimen bears a superficial resemblance to the Mycetozoon genus *Craterium*.

The genus represents a morphological variation of the normal structure of *Orbitolites complanata*. In that type the chamberlets form a disc, the sides of which are imperforate, while the edge of the disc is covered with cribrate apertures. In *Craterites* the disc is originally perforate on one side and imperforate round the edge. Growth ensues by the addition of a series of chambers, which must necessarily be superimposed over the aperture. Hence we get a series of discs superimposed on one another and with a circular cribrate covering over all in *Craterites*, while in *Orbitolites* the original disc increases rapidly in diameter by the addition of rings of concentric chamberlets.

Size :—

Height from edge of base to top of cover, 1·20 mm.

„ „ bottom of cover, ·70 mm.

Diameter at base, ·95 mm.

„ narrowest part of trunk, ·55 mm.

„ widest part of trunk and junction of cover, ·95 mm.

#### ALVEOLINA d'Orbigny.

##### 58. ALVEOLINA MELO (*Fichtel & Moll*).

*Nautilus melo* Fichtel & Moll, 1798, TM. p. 118, pl. 24.

*Alveolina* „ Heron-Allen & Earland, 1914-15, FKA. p. 607.

A single large specimen.

#### Family ASTRORHIZIDÆ.

##### Sub-family ASTRORHIZINÆ.

##### IRIDIA *Heron-Allen & Earland*.

##### 59. IRIDIA DIAPHANA *Heron-Allen & Earland*.

*Iridia diaphana* Heron-Allen & Earland, 1914-15, FKA. 1914, p. 371, pl. 36 ;  
1915, p. 607.

The species is evidently abundantly attached to coral and nullipore fragments. Several good specimens were obtained, both sessile and detached, the latter exhibiting the dried protoplasmic body beneath the chitinous membrane.

DENDROPHRYA *Strethill Wright*.60. DENDROPHRYA RADIATA *Strethill Wright* (?).

*Dendrophrya radiata* Strethill Wright, 1861, Ann. & Mag. Nat. Hist. ser. 3,  
vol. viii. p. 122. (*No figure*.)

„ „ Brady, 1884, FC. p. 238, pl. 27 A. figs. 10-12.

Two large fragments which we ascribe to *Dendrophrya*, to which they bear a closer resemblance than to any other species. They represent fragments of an organism constructed of irregularly branching flattened tubes, formed of fine brown sand deposited upon a chitinous membrane. The interior of the tubes is more or less rough (semi-labyrinthic) with projecting material. The internal calibre of the tube is very large, the walls being comparatively thin. In the absence of further material we are unable to assign these fragments to any of the recorded species, and hesitate to give them a new name. It may be that our organism represents fragments of Cushman's suggested species *Dendrophrya ramosa* or its var. *robusta*. (C. 1921, FP. p. 56, pl. 18. figs. 7, 8.)

## Sub-family RHABDAMMININÆ.

SAGENINA *Chapman*.61. SAGENINA FRONDESCENS (*Brady*).

*Sagenella frondescens* Brady, 1879, etc., RRC. 1879, p. 41, pl. 5. fig. 1.

*Sagenina* „ Chapman, 1899, FFA. p. 4, pl. 1. figs. 1, 2; pl. 2. figs. 1, 2.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 611.

Large and typical colonies attached to small stones.

## Family LITUOLIDÆ.

## Sub-family LITUOLINÆ.

HAPLOPHRAGMIUM *Reuss*.62. HAPLOPHRAGMIUM COMPRESSUM (*Goës*).

*Lituolina irregularis*, var. *compressa* Goës, 1882, RRCS. p. 141, pl. 12.  
figs. 421-423.

*Haplophragmium emaciatum* Brady, 1884, FC. p. 305, pl. 33. figs. 26-28.

„ *compressum* Goës, 1896, DOA. p. 31.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 613,  
pl. 46. figs. 20, 21.

A single small and coarsely agglutinate specimen.

63. HAPLOPHRAGMIUM CANARIENSE (*d'Orbigny*).

*Nonionina canariensis* d'Orbigny, 1839, FIC. p. 128, pl. 2. figs. 33, 34.

*Haplophragmium canariense* Brady, 1884, FC. p. 310, pl. 35. figs. 1-5.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 614.

Common, and attaining large dimensions. Characterized by a thin white regular test, deeply ferruginous, and very neatly constructed of fine sand with a very considerable proportion of sponge-spicules.

64. *HAPLOPHRAGMIUM ANCEPS* Brady.

*Haplophragmium anceps* Brady, 1884, FC. p. 313, pl. 35. figs. 12-15.

„ „ Millett, 1898, etc., FM. 1899, p. 361, pl. 5. fig. 10.

„ „ Heron-Allen & Earland, 1913, CL. p. 47, pl. 3. fig. 4.

Two small, but typical specimens.

PLACOPSILINA *d'Orbigny*.

65. *PLACOPSILINA CENOMANA d'Orbigny*.

*Placopsilina cenomana* d'Orbigny, 1850, etc., PP. vol. ii. p. 185, no. 758.

*Lituola (Placopsilina) cenomana* Carpenter, Parker, & Jones, 1862, ISF. p. 143 pl. 11. fig. 14.

*Placopsilina* „ „ Brady, 1884, FC. p. 315, pl. 36. figs. 1-3

A number of fragments agreeing in structure with this species, but all "free." It is possible that they may have been originally sessile upon some perishable organism.

DIFFUSILINA *Heron-Allen & Earland*.

DIFFUSILINA, *gen. nov.*

Test sessile, squamous, composed of very finely comminuted sand and mud enveloping a thin labyrinthic layer of chambers. External surface smooth and finished, white to grey in colour, furnished with a few sparsely distributed pustules of more loosely aggregated material.

The fragments of calcareous alga furnished many examples of this new type. It is at first very difficult to recognize owing to its colour harmonizing with that of its host. Its squamous form and habit of growing only in depressions and crevices of the alga add to the difficulty of detecting it, but when once recognized its presence can hardly be overlooked. It may possibly be a widely distributed type.

The affinities of *Diffusilina* are not easily discoverable. The neatly constructed test and high proportion of cement in the finished exterior surface indicate the Lituolidæ, but it has no close relationship to any previously recorded type. We suggest *Bdelloidina* as its nearest, but still a distant, ally.

66. *DIFFUSILINA HUMILIS*, sp. nov. (Pl. 35. figs. 13-16.)

Test sessile, of irregular outline, squamous, adapting its growth to depressions and crevices on the surface of its host (*diffusus*=poured out, spilled). Colour resembling its host, white to grey. External surface smoothly finished and flat; marginal edges thinned out so as to appear

almost continuous with the surface of attachment and presenting no sign of marginal apertures. Nearly all the specimens exhibit a varying number (1-4) of pustular processes on the superior surface. These rise slightly above the smoothly finished agglutinate surface, and appear to consist of the same fine sand and mud as the rest of the test, but without agglutinating cement. It appears probable that they represent apertures for the extension of protoplasm.

The test when laid open is seen to contain a single layer of intricately ramifying flat tubes, without septa, separated from one another by thin walls of agglutinated material and from the surface of the alga by a thin floor or pavement layer of similar material. The tubes are completely filled with a mass of dark protoplasm. The protoplasmic body is voluminous, dark in colour, and ramifies through the entire structure in a single layer separated from the surface of the alga by a floor of material similar to that used in the construction of the upper layer of the test.

Size very variable. Compact specimens 1-3 mm. in diameter, but narrow specimens following a crevice in their growth may probably attain four or five times this size.

#### HADDONIA Chapman.

##### 67. HADDONIA TORRESIENSIS Chapman. (Pl. 35. figs. 17-22.)

*Haddonina torresiensis* Chapman, 1897, "On *Haddonina*, a new Genus of the Foraminifera from Torres Straits," Journ. Linn. Soc. Lond. vol. xxvi. (Zoology) (1898) pp. 452-456, pl. 28. & text-fig. p. 453.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 616, pl. 46. fig. 22.

Abundant and extremely variable both as regards size and relative irregularity of growth. This organism, which is so abundant in this material, appears to be unquestionably referable to Chapman's genus; but a study of the material leads us to differ from his conclusions as to its relationships. He placed his genus among the labyrinthic Lituolinæ; we feel inclined to transfer it to the Textulariidae, and we have even some doubt as to its generic value. A study of a series of specimens indicates that at Lord Howe Island growth starts as a free and regularly formed *Textularia* (*agglutinans* or *gramen*). After attaining almost full growth the chambers begin to run wild, and they may then assume practically any form—curving or straight lines, acervuline masses, remain free, attach themselves to large sand-grains, or become sessile upon other organisms, but often so lightly as to become detached without damage. The shell-structure is of coarse calcareous and siliceous grains with a large proportion of calcareous cement. Chapman states that "the test commences either with a straight or a sinuous series of chambers, or, more rarely, with a flat coil of a single whorl, after which the

chambers are arranged in a more or less rectilinear manner." In only one or two instances have we met with a coiled initial series. But for the established existence of *Haddonina* as a genus, and the fact that the Lord Howe specimens generally coincide with Chapman's diagnosis, we should have regarded our specimens as biological freaks, due perhaps to brackish-water conditions affecting the growth of the characteristic *Textularia* of the district, as such conditions of life have been proved to do.

### Sub-family TROCHAMMININÆ.

#### TROCHAMMINA Parker & Jones.

##### 68. TROCHAMMINA SQUAMATA Parker & Jones.

*Trochammina squamata* Parker & Jones, 1860, RMF. p. 304, table.

" " Brady, 1884, FC. p. 337, pl. 41. fig. 3.

" " Heron-Allen & Earland, 1913, CI. p. 50, pl. 3. figs. 7-10.

Small, pauperate, and very rare.

##### 69. TROCHAMMINA OCHRACEA (Williamson).

*Rotalina ochracea* Williamson, 1858, RFGB. p. 55, pl. 4. fig. 112; pl. 5. fig. 113.

*Trochammina* " Millett, 1898, etc., FM. 1899, p. 363, pl. 5. fig. 12.

" " Heron-Allen & Earland, 1914-15, FKA. p. 619, pl. 46. figs. 27, 28.

One extremely pauperate individual, showing the flange described by us from Kerimba (*ut supra*), and two small but typical specimens.

##### 70. TROCHAMMINA ROTALIFORMIS Wright.

*Trochammina inflata*, var., Balkwill & Wright, 1885, DIS. p. 331, pl. 13. figs. 11, 12.

" *rotaliformis* Heron-Allen & Earland, 1913, CI. p. 52, pl. 3. figs. 11-13.

Frequent and well-developed.

##### 71. TROCHAMMINA VESICULARIS Goës.

*Trochammina vesicularis* Goës, 1894, ASF. p. 31, pl. 6. figs. 235-237.

One large and typical specimen of this high-domed type.

#### CARTERINA Brady.

##### 72. CARTERINA SPICULOTESTA (Carter).

*Rotalia spiculotesta* H. J. Carter, 1877, "Description of a new Species of Foraminifera (*Rotalia spiculotesta*)," Ann. & Mag. Nat. Hist. ser. 4, vol. xx. p. 470, pl. 16; 1879, ser. 5, vol. iii. p. 414; 1880, SGM. ser. 5, vol. v. p. 452.

*Carterina spiculotesta* Brady, 1884, FC. p. 346, pl. 41. figs. 7-10.

" " Sidebottom, 1906, etc., RFD. 1905, p. 6, pl. 1. fig. 10.

A single undoubted fragment, representing a terminal chamber. The individual when perfect must have been of considerable size.

### Family TEXTULARIIDÆ.

#### Sub-family TEXTULARIINÆ.

##### TEXTULARIA *DeFrance*.

#### 73. TEXTULARIA FOLIUM *Parker & Jones*.

*Textularia folium* Parker & Jones, 1865, NAAF. pp. 370 & 450, pl. 18. fig. 19.

" " Brady, 1884, FC. p. 357, pl. 42. figs. 1-5.

" " Chapman, 1907, RFV. p. 127, pl. 9. fig. 4.

A single specimen.

#### 74. TEXTULARIA INCONSPICUA, var. JUGOSA (*Brady*).

*Textularia jugosa* Brady, 1884, FC. p. 358, pl. 42. fig. 7.

" *inconspicua*, var. *jugosa* Millett, 1898, etc., FM. 1899, p. 558, pl. 7. fig. 2.

" " " Heron-Allen & Earland, 1908, etc., SB. 1911, p. 310, pl. 9. fig. 12; 1914-15, FKA. p. 624.

One typical specimen.

#### 75. TEXTULARIA RHOMBOIDALIS *Millett*.

*Textularia rhomboidalis* Millett, 1898, etc., FM. 1899, p. 559, pl. 7. fig. 4.

" " Sidebottom, 1904, etc., RFD. 1905, p. 8, pl. 2. figs. 2, ? 3.

" " Heron-Allen & Earland, 1914-15, FKA. p. 624.

Very abundant and very variable, the marginal edges ranging from quite straight to strongly scalloped, owing to the projection of the extremities of the chambers. The median line is often deeply excavated. Small specimens are often so compressed as to be with difficulty separated from *Bolivina*. Limbation of the sutural lines often gives a highly decorative appearance to the shell.

#### 76. TEXTULARIA CRISPATA *Brady*.

*Textularia crispata* Brady, 1884, FC. p. 359, pl. 113. fig. 2.

" " Heron-Allen & Earland, 1914-15, FKA. p. 624, pl. 47. figs. 5, 6.

Two specimens, one very large and quite typical, the other small.

77. *TEXTULARIA SAGITTULA DeFrance.*

*Textularia sagittula* DeFrance, 1824, Dict. Sci. Nat. vol. xxxii. p. 177; vol. liii. p. 344; Atlas Conch. pl. 13. fig. 5.

" " Brady, 1884, FC. p. 361, pl. 42. figs. 17, 18.

" " Heron-Allen & Earland, 1914-15, FKA. p. 625.

Very rare.

78. *TEXTULARIA SAGITTULA*, var. *FISTULOSA* Brady.

*Textularia sagittula*, var. *fistulosa* Brady, 1884, FC. p. 362, pl. 42. figs. 19-22.

" " " Millett, 1898, etc., FM. 1899, p. 561, pl. 7. fig. 9.

Also rare and small.

79. *TEXTULARIA RUGOSA (Reuss).*

*Plecanium rugosum* Reuss, 1869, FOG. p. 453, pl. 1. fig. 3.

*Textularia rugosa* Brady, 1884, FC. p. 625, pl. 42. figs. 23, 24.

" " Heron-Allen & Earland, 1914-15, FKA. p. 625, pl. 47. figs. 7-9.

Large, but not very strongly marked.

80. *TEXTULARIA AGGLUTINANS d'Orbigny.*

*Textularia agglutinans* d'Orbigny, 1839, FC. p. 144, pl. 1. figs. 17, 18, 32-34.

" " Brady, 1884, FC. p. 363, pl. 43. figs. 1-3.

" " Heron-Allen & Earland, 1914-15, FKA. p. 626.

Abundant and subject to much variation in the direction of irregular growth, suggestive of incipient progress towards *Haddonina*, q. v.

81. *TEXTULARIA CANDEIANA d'Orbigny.*

*Textularia candeiana* d'Orbigny, 1839, FC. p. 143, pl. 1. figs. 25-27.

" " Sidebottom, 1904, etc., RFD. 1905, p. 7, pl. 2. fig. 1.

" " Heron-Allen & Earland, 1914-15, FKA. p. 627, pl. 47. figs. 10-16.

Not uncommon, but not very strongly developed or typical.

82. *TEXTULARIA ABBREVIATA d'Orbigny.*

*Textularia abbreviata* d'Orbigny, 1846, FFV. p. 249, pl. 15. figs. 9-12 (not 7-12).

" *agglutinans*, var. *abbreviata* Parker & Jones, 1865, NAAF. p. 369, pl. 17. fig. 76.

" *abbreviata* Heron-Allen & Earland, 1922, T.N. p. 120.

One large stoutly built specimen.

83. *TEXTULARIA GRAMEN d'Orbigny.*

*Textularia gramen* d'Orbigny, 1846, FFV. p. 248, pl. 15. figs. 4-6.

" " Brady, 1884, FC. p. 365, pl. 43. figs. 9, 10.

" " Heron-Allen & Earland, 1914-15, FKA. p. 627.

Common, and exhibiting the same tendency to *Haddonia*-formation as *T. agglutinans*.

84. *TEXTULARIA CONICA* d'Orbigny.

*Textularia conica* d'Orbigny, 1839, FC. p. 143, pl. 1. figs. 19, 20.

" " Brady, 1884, FC. p. 365, pl. 43. figs. 13, 14; pl. 113. fig. 1.

" " Heron-Allen & Earland, 1914-15, FKA. p. 629.

Common.

85. *TEXTULARIA CONICA*, var. *JUGOSA* Jones & Millett.

*Textularia sagittula*, var. *jugosa* Jones; Millett, 1898, etc., FM. 1809, p. 561, pl. 7. fig. 8.

A few small specimens comparable with Millett's figure (*ut supra*), which appears to us to be referable to *T. conica* rather than to *T. sagittula*.

*VERNEUILINA* d'Orbigny.

86. *VERNEUILINA SPINULOSA* Reuss.

*Verneuilina spinulosa* Reuss, 1849-50, FOT. p. 374, pl. 2. (47) fig. 12.

" " Brady, 1884, FC. p. 384, pl. 47. figs. 1-3.

" " Heron-Allen & Earland, 1914-15, FKA. p. 630.

Not uncommon. All the specimens are of the broad heavy type, destitute of spines.

87. *VERNEUILINA POLYSTROPHA* (Reuss).

*Bulimina polystropha* Reuss, 1845-46, VBK. pt. 2, p. 109, pl. 24. fig. 53.

*Verneuilina* " Brady, 1884, FC. p. 386, pl. 47. fig. 9.

" " Heron-Allen & Earland, 1929, VP. (*passim*).

Minute and very rare.

88. *VERNEUILINA PROPINQUA* Brady.

*Verneuilina propinqua* Brady, 1884, FC. p. 387, pl. 47. figs. 8-12 (not 13, 14).

" " Cushman, 1910, etc., FNP. 1911, p. 56, fig. 92.

A single minute but typical specimen.

*TRITAXIA* Reuss.

89. *TRITAXIA LEPIDA* Brady.

*Tritaxia lepida* Brady, 1879, etc., RRC. 1881, p. 55.

" " Brady, 1884, FC. p. 389, pl. 49. fig. 12.

" " Millett, 1898, etc., FM. 1900, p. 12, pl. 1. fig. 15.

Frequent.

*PAYONINA* d'Orbigny.

90. *PAYONINA FLABELLIFORMIS* d'Orbigny.

*Pavonina flabelliformis* d'Orbigny, TMC. p. 260, no. 1, pl. 10. figs. 10, 11; Modèle, no. 56.



*Pavonina flabelliformis* Brady, 1884, FC. p. 374, pl. 45. figs. 17-21.

" " Heron-Allen & Earland, 1914-15, FKA. p. 632,  
pl. 48. figs. 1-6.

One broken specimen which, when perfect, must have been of very large size.

#### SPIROPLECTA Ehrenberg.

##### 91. SPIROPLECTA BIFORMIS (Parker & Jones).

*Textularia agglutinans*, var. *biformis* Parker & Jones, 1865, NAAF. p. 370,  
pl. 15. figs. 23, 24.

*Spiroplecta biformis* Brady, 1884, FC. p. 376, p. 45. figs. 25-27.

" " Heron-Allen & Earland, 1914-15, FKA. p. 634.

One typical specimen.

#### GAUDRYINA d'Orbigny.

##### 92. GAUDRYINA SCABRA Brady.

*Gaudryina scabra* Brady, 1884, FC. p. 381, pl. 12. fig. 5.

" " Heron-Allen & Earland, 1914-15, FKA. p. 635, pl. 48.  
figs. 7-14.

Rare. The specimens are small, but compare in all respects with those figured by us (*ut supra*). We there suggested that they might be multiform variations of *Verneuilina polystropha*, and the Lord Howe specimens confirm that view.

##### 93. GAUDRYINA RUGOSA (d'Orbigny).

*Gaudryina rugosa* d'Orbigny, 1840, CBP. p. 44, pl. 4. figs. 20, 21.

" " Brady, 1884, FC. p. 381, pl. 46. figs. 14-16.

" " Heron-Allen & Earland, 1914-15, FKA. p. 635; 1922,  
TN. p. 122.

Very common and finely developed. As in the New Zealand area, two distinct types occur, to which we have called attention in our 'Terra Nova' Report (*ut supra*), one long and the other short.

#### Subfamily BULIMININÆ.

##### BULIMINA d'Orbigny.

##### 94. BULIMINA ELEGANTISSIMA d'Orbigny. (Pl. 35. figs. 23, 24.)

*Bulimina elegantissima* d'Orbigny, 1839, FAM. p. 51, pl. 7. figs. 13, 14.

" " Brady, 1884, FC. p. 402, pl. 50. figs. 20-22.

" " Heron-Allen & Earland, 1914-15, FKA. p. 639.

Rare, but characteristic, and an interesting series; two specimens exhibiting budding-off tests, of one and two chambers respectively, precisely similar to those figured by Heron-Allen (1915, RPF), and by Sidebottom.

under the type-species *B. elegantissima* (S. 1904, etc., RFD. 1905, p. 11, pl. 2. figs. 7-12), also a specimen in which the terminal septal face and terminal septa have been absorbed.

95. *BULIMINA WILLIAMSONIANA* *Brady*.

*Bulimina williamsoniana* Brady, 1884, FC. p. 408, pl. 51. figs. 16, 17.

" " Millett, 1898, etc., FM. 1900, p. 279, pl. 2. fig. 8.

" " Heron-Allen & Earland, 1914-15, FKA. p. 641.

One very minute specimen.

*BOLIVINA d'Orbigny*.

96. *BOLIVINA PUNCTATA* *d'Orbigny*.

*Bolivina punctata* d'Orbigny, 1839, FAM. p. 63, pl. 8. figs. 10-12.

" " Brady, 1884, FC. p. 417, pl. 52. figs. 18, 19.

" " Heron-Allen & Earland, 1914-15, FKA. p. 644.

Common, but rather weakly developed.

97. *BOLIVINA TEXTILARIOIDES* *Reuss*.

*Bolivina textilarioides* Reuss, 1862, NHG. p. 81, pl. 10. fig. 1.

" " Brady, 1884, FC. p. 419, pl. 52. figs. 23-25.

" " Heron-Allen & Earland, 1914-15, FKA. p. 645.

Rare and small. A variety also occurs in greater numbers, characterized by a broad compressed shell with rounded aboral extremity; five or six pairs of chambers, separated by strongly limbate sutural lines. The parallel arrangement of these lines indicates its affinity to *B. textilarioides*, but it differs considerably from the type. The form is not infrequent in tropical shallow-water gatherings.

98. *BOLIVINA DILATATA* *Reuss*.

*Bolivina dilatata* Reuss, 1849-50, FOT. p. 381, pl. 3. (48) fig. 15.

" " Brady, 1884, FC. p. 418, pl. 52. figs. 20, 21.

" " Heron-Allen & Earland, 1914-15, FKA. p. 645.

Rare and far from typical.

99. *BOLIVINA TORTUOSA* *Brady*.

*Bolivina tortuosa* Brady, 1884, FC. p. 420, pl. 52. figs. 31-34.

" " Heron-Allen & Earland, 1913, CI. p. 66, pl. 5. fig. 1; 1914-15, FKA. p. 645.

Large and well-developed, but rare.

100. *BOLIVINA ROBUSTA* *Brady*.

*Bolivina robusta* Brady, 1884, FC. p. 421, pl. 53. figs. 7-9.

" " Heron-Allen & Earland, 1914-15, FKA. p. 646.

One very small but otherwise typical specimen

101. *BOLIVINA LIMBATA* Brady.*Bolivina limbata* Brady, 1884, FC. p. 419, pl. 52. figs. 26-28

„ „ Heron-Allen & Earland, 1913, CI. p. 67, pl. 5. figs. 2, 3;  
1914-15, FKA. p. 646, pl. 50. figs. 1-4.

Rare, but large and well-developed. Most of the specimens are bifarine in their later development.

102. *BOLIVINA LIMBATA*, var. *ABBREVIATA*, nov. (Pl. 36. figs. 25-27.)

Test compressed, consisting of 4 to 7 pairs of chambers with rounded marginal edges, heavily limbate but with flush sutures. Aboral extremity rounded. The shell reaches its maximum breadth at about the third pair of chambers, and therefore the sides are almost parallel. Aperture large, extending over the septal face of the final chamber. Surface of the chambers prominently perforate between the clear sutural lines.

This is a very easily recognized little form, and not uncommon in shallow-water tropical gatherings. It may represent an intermediate type between *B. textularioides* (which it resembles in the straight sutural lines, almost vertical to the long axis) and the typical *B. limbata*. It never, so far as we have observed, has that tendency to develop a bifarine terminal portion so characteristic of the latter species.

103. *BOLIVINA VARIABILIS* (Williamson).*Textularia variabilis* (typica) Williamson, 1858, RFGB. p. 76, pl. 6. figs. 162, 163.*Bolivina* „ Heron-Allen & Earland, 1914-15, FKA. p. 647.

The most typical *Bolivina* of the gathering, frequent, well-developed, and exhibiting a considerable range in the extent of the surface-markings.

104. *BOLIVINA Plicata* d'Orbigny.*Bolivina plicata* d'Orbigny, 1839, FAM. p. 62, pl. 8. figs. 4-7.

„ „ Goes, 1894, ASF. p. 51, pl. 9. figs. 487, 488.

Two specimens, very strongly marked.

105. *BOLIVINA INFLATA* Heron-Allen & Earland.

*Bolivina inflata* Heron-Allen & Earland, 1913, CI. p. 68, pl. 4. figs. 16-19;  
1916, F.W.S. p. 240.

Not uncommon and quite typical.

## Sub-family CASSIDULININÆ.

## CASSIDULINA d'Orbigny.

106. *CASSIDULINA CRASSA* d'Orbigny.*Cassidulina crassa* d'Orbigny, 1839, FAM. p. 56, pl. 7. figs. 18-20.

*Cassidulina crassa* Brady, 1884, FC. p. 429, pl. 54. figs. 4, 5.

" " Cushman, 1910, etc., FNP. 1911, p. 97, fig. 151.

Rare and very small.

107. *CASSIDULINA SUBGLOBOSA* Brady.

*Cassidulina subglobosa* Brady, 1884, FC. p. 430, pl. 54. fig. 17.

" " Cushman, 1910, etc., FNP, 1911, p. 98, fig. 152.

" " Heron-Allen & Earland, 1914-15, FKA. p. 652.

Frequent, occurring in two distinct forms, one very small and hyaline, the other much larger (up to three times the size) and with a matt surface. The second form presents the same external characteristics even in the immature condition, and we are unable to offer any explanation of this condition. They are not dead or eroded shells.

108. *CASSIDULINA (ORTHOPECTA) CLAVATA* Brady.

*Cassidulina (Orthoplecta) clavata* Brady, 1884, FC. p. 432, pl. 113. fig. 9.

" " " Chapman, 1901, FFA. (1902) p. 402 (list), no. 114.

" " " Heron-Allen & Earland, 1914-15, FKA. p. 654, pl. 50. figs. 21, 22.

One small specimen of this very rare shallow-water tropical type.

*EHRENBERGINA* Reuss.

109. *EHRENBERGINA SERRATA* Reuss.

*Ehrenbergina serrata* Reuss, 1849-50, FOT. p. 377, pl. 48. fig. 7.

" " Cushman, 1910, etc., FNP. 1911, p. 101, fig. 155.

" " Heron-Allen & Earland, 1922, TN. p. 140.

Rare. The specimens are small, with extremely pronounced, raised, limbate sutures. Immature specimens are hardly distinguishable from the figure of *Cassidulina elegans* Sidebottom (S. 1910, J. Quekett Micr. Cl. ser. 2, vol. xi. p. 106, pl. 4. fig. 1), to which, perhaps, we should have ascribed them in the absence of the mature and more typical individuals.

Family *LAGENIDÆ*.

Sub-family *LAGENINÆ*.

*LAGENA* Walker & Boys.

110. *LAGENA LINEATA* (Williamson).

*Entosolenia lineata* Williamson, 1848, BSGL. p. 18, pl. 2. fig. 18.

*Lagena* " Brady, 1884, FC. p. 461, pl. 57. fig. 13.

" " Heron-Allen & Earland, 1914-15, FKA. p. 656.

One typical specimen.

111. *LAGENA SQUAMOSA* (Montagu).

*Vermiculum squamosum* Montagu, 1803, TB. p. 526, pl. 14. fig. 2.

*Lagena squamosa* Cushman, 1910, etc., FNP. 1913, p. 16, pl. 6. fig. 1.

" " Heron-Allen & Earland, 1922, TN. p. 151, pl. vi. figs. 1, 2.

One abnormal, thick-shelled, and weakly marked individual.

112. *LAGENA LÆVIS* (Montagu).

*Vermiculum laeve* Montagu, 1803, TB. p. 524.

*Lagena laevis* Williamson, 1848, BSGL. p. 12, pl. 1. figs. 1, 2.

" " Brady, 1884, FC. p. 455, pl. 56. figs. 7-14, 30.

One abnormal specimen, the aboral half of which is very irregularly formed.

113. *LAGENA LÆVIGATA* (Reuss).

*Fissurina laevigata* Reuss, 1849-50, FOT. p. 366, pl. 1. (46) fig. 1.

*Lagena* " Brady, 1884, FC. p. 473, pl. 114. fig. 8.

" " Heron-Allen & Earland, 1914-15, FKA. p. 661.

One specimen with a hooded aperture resembling Sidebottom's fig. 7 on pl. 17 (S. 1912, LSP. p. 400), which he considers to be allied to *L. millettii* Uhaster (C. 1892, FS. p. 61, pl. 1. fig. 10). The Lord Howe specimen has a normal aboral base. A good many small specimens also of the typical form.

114. *LAGENA ANNECTENS* Burrows & Holland.

*Lagena annectens* Burrows & Holland, in J., P., & B. 1866, etc., MFC. 1895, p. 203, pl. 7. fig. 11.

" " Heron-Allen & Earland, 1922, TN. p. 155.

One small weak specimen.

115. *LAGENA MARGINATA* (Walker & Boys).

*Serpula (Lagena) marginata* Walker & Boys, 1784, TMR. p. 2, pl. 1. fig. 7.

*Lagena marginata* Brady, 1884, FC. p. 476, pl. 59. figs. 21-23.

" " Heron-Allen & Earland, 1914-15, FKA. p. 663.

Many small fully marginated specimens.

116. *LAGENA BICARINATA* (Terquem).

*Fissurina bicarinata* Terquem, 1882, FEP. p. 31, pl. 1. (9) fig. 24.

*Lagena* " Millett, 1895, etc., FM. 1901, p. 624, pl. 14. fig. 13.

" " Heron-Allen & Earland, 1914-15, FKA. p. 665.

One minute specimen.

117. *LAGENA OLATHRATA* Brady.

*Lagena olathrata* Brady, 1884, FC. p. 485, pl. 60. fig. 4.

" " Heron-Allen & Earland, 1913, OL. p. 90, pl. 7. fig. 10.

One very feebly costate specimen.

## Sub-family NODOSARIINÆ.

## FRONDICULARIA Defrance.

## 118. FRONDICULARIA SCOTTII Heron-Allen &amp; Earland. (Pl. 36. figs. 28, 29.)

*Frondicularia scottii* Heron-Allen & Earland, 1922, TN. p. 175, pl. 6.  
figs. 30-32.

One small and feeble example which we have no hesitation in ascribing to this species. It lacks the longitudinal grooves and decorations of the type, but it has the same truncate edges and thick shell-wall, which obscures the internal structure. This is brought out by wetting the specimen. The occurrence of this individual in a shore sand is very noteworthy; it is practically identical in size with the pauperate specimen from Raine Island, recorded by us *ut supra*, but is even weaker, having no limbation of the sutural lines. We figure both the Lord Howe and Raine Island specimens.

## CRISTELLARIA Lamarck.

## 119. CRISTELLARIA ROTULATA (Lamarck).

*Lenticulites rotulata* Lamarck, 1804, AM. p. 188, no. 3; 1830, EM. p. 330,  
pl. 466. fig. 5.

*Cristellaria* „ Brady, 1881, FC. p. 517, pl. 49. fig. 13.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 671.

Rare and rather small, but typical.

## 120. CRISTELLARIA GIBBA d'Orbigny.

*Cristellaria gibba*, d'Orbigny, 1839, FC. p. 40, pl. 7. figs. 20, 21.

„ „ Brady, 1884, FC. p. 546, pl. 60. figs. 8, 9.

„ „ Cushman, 1910, etc., FNP. 1913, p. 69, pl. 35. fig. 1.

One weak specimen.

## Sub-family POLYMORPHININÆ.

## POLYMORPHINA d'Orbigny.

## 121. POLYMORPHINA COMMUNIS d'Orbigny.

*Polymorphina (Guttulina) communis* d'Orbigny, 1826, TMC. p. 266,  
nos. 14, 15, pl. 12. figs. 1-4; Modèles, nos. 61, 62.

„ *communis* Brady, 1884, FC. p. 568, pl. 72. fig. 19.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 673.

A single small specimen.

## 122. POLYMORPHINA PROBLEMA d'Orbigny.

*Polymorphina (Guttulina) problema* d'Orbigny, 1826, TMC. p. 266, no. 14;  
Modèle, no. 61.

*Polymorphina problema* Brady, 1884, FC. p. 568, pl. 72. fig. 20; pl. 73, fig. 1.

" " Heron-Allen & Earland, 1922, TN. p. 182.

A single small specimen.

123. *POLYMORPHINA REGINA* Brady, Parker, & Jones.

*Polymorphina regina* Brady, Parker, & Jones, 1870, GP. p. 241, pl. 41. fig. 32.

" " Brady, 1884, FC. p. 571, pl. 73. figs. 11-13.

" " Cushman, 1910, etc., FNP. 1913, p. 91, pl. 41. figs. 6, 7.

One very large broken specimen and one of normal size.

*UVIGERINA d'Orbigny.*

124. *UVIGERINA PYGMÆA d'Orbigny.*

*Uvigerina pygmæa* d'Orbigny, 1826, TMC. p. 269, pl. 12. figs. 8, 9; Modèle, no. 67.

" " Brady, 1884, FC. p. 575, pl. 74. figs. 11, 12.

" " Heron-Allen & Earland, 1914-15, FKA. p. 675

Three rather small specimens with very strong costation.

125. *UVIGERINA PORRECTA* Brady.

*Uvigerina porrecta* Brady, 1879, etc., RRC. 1879, p. 274, pl. 8. figs. 15, 16.

" " Brady, 1884, FC. p. 577, pl. 74. figs. 21-23.

" " Heron-Allen & Earland, 1914-15, FKA. p. 675.

Frequent and typical.

126. *UVIGERINA SELSEYENSIS* Heron-Allen & Earland.

*Uvigerina selseyensis* Heron-Allen & Earland, 1908, etc., SB. 1909, p. 437, pl. 18. figs. 1-3.

" " Cushman, 1910, etc., FNP. 1913, p. 93, pl. 42. fig. 5.

Several specimens resembling the Eocene fossils recorded by us (*ut supra*), in the shape and arrangement of the chambers, but with a rough, feebly hispid or striate surface.

127. *UVIGERINA ANGULOSA* Williamson.

*Uvigerina angulosa* Williamson, 1858, RFGB. p. 67, pl. 5. fig. 140.

" " Brady, 1884, FC. p. 576, pl. 74. figs. 15-18.

" " Heron-Allen & Earland, 1914-15, FKA. p. 676.

Frequent and large. Two separate forms occur, one very long, the other short and rapidly increasing in breadth.

*SAGRINA* Parker & Jones.

128. *SAGRINA COLUMELLARIS* Brady.

*Sagrina columellaris* Brady, 1884, FC. p. 581, pl. 75. figs. 15-17.

" " Cushman, 1910, etc., FNP. 1913, p. 104, pl. 47. figs. 2, 3.

" " Heron-Allen & Earland, 1914-15, FKA. p. 676.

Rare, but typical.

129. *SAGRINA RAPHANUS* *Parker & Jones.*

*Uvigerina (Sagrina) raphanus* Parker & Jones, 1865, NAAF. p. 364, pl. 18.  
figs. 16, 17.

*Sagrina raphanus* Brady, 1884, FC. p. 585, pl. 75. figs. 21-24.

" " Heron-Allen & Earland, 1914-15, FKA. p. 677.

Rare, large, of the entosolenian type.

## Sub-family RAMULININÆ.

RAMULINA *Rupert Jones.*130. *RAMULINA GRIMALDII* *Schlumberger.* (Pl. 36. fig. 32.)

*Ramulina grimaldii* Schlumberger, 1891, Mém. Soc. Zool. France, vol. iv.  
pp. 509-511, pl. 5.

*Ramulina*? Heron-Allen & Earland, 1922, TN. p. 187, text-fig.

The occurrence in this material of a specimen practically identical in formation with the one recorded by us (*ut supra*) from New Zealand seems to render it necessary to give it a specific name, a task which we have hitherto avoided. Rather than make a new species on such insufficient material, we have decided to use Schlumberger's name. The organism described and figured by Flint as *R. proteiformis* (F. 1899, RFA. p. 321, pl. 68. fig. 7) appears to be a simpler form of the same kind and possibly identical with Schlumberger's species.

## Family GLOBIGERINIDÆ.

GLOBIGERINA *d'Orbigny.*131. *GLOBIGERINA BULLOIDES* *d'Orbigny.*

*Globigerina bulloides* d'Orbigny, 1826, TMC. p. 277, no. 1; Modèles, nos. 17, 76.

" " Brady, 1884, FC. p. 593, pls. 77 & 79. figs. 3-7.

" " Heron-Allen & Earland, 1914-15, FKA. p. 678.

The specimens are small and few in number.

132. *GLOBIGERINA TRILOBA* *Reuss.*

*Globigerina triloba* Reuss, 1849-50, FOT. p. 374, pl. 2. (47) fig. 11.

" " Brady, 1884, FC. p. 595, pl. 79. figs. 1, 2; pl. 81. figs. 2, 3.

" " Heron-Allen & Earland, 1914-15, FKA. p. 678.

More frequent, larger, and better developed than *G. bulloides*.

133. *GLOBIGERINA CRETACEA*, var. *EGGERI* *Heron-Allen & Earland.*

*Globigerina cretacea*, var. *eggeri* Heron-Allen & Earland, 1922, TN. p. 188,  
pl. 7. figs. 6-8.

Two small but typical individuals.



134. *GLOBIGERINA RUBRA d'Orbigny.**Globigermna rubra* d'Orbigny, 1839, FC. p. 82, pl. 4. figs. 12-14.

" " Brady, 1884, FC. p. 602, pl. 79. figs. 11-16.

" " Heron-Allen &amp; Earland, 1914-15, FKA. p. 679.

Large and not infrequent, but devoid of the characteristic colouring.

## Family ROTALIIDÆ.

## Subfamily SPIRILLININÆ.

SPIRILLINA *Lhrenberg.*135. *SPIRILLINA VIVIPARA Ehrenberg.**Spirillina vivipara* Ehrenberg, 1841, SNA. p. 442, pl. 3 fig. 41.

" " Brady, 1884, FC. p. 640, pl. 85. figs. 1-5.

" " Heron-Allen &amp; Earland, 1914-15, FKA. p. 683, pl. 51. figs. 19-23.

Frequent, and presenting the usual wide range of breadth of tube and number of convolutions.

136. *SPIRILLINA LIMBATA Brady.**Spirillina limbata* Brady, 1879, RRÇ p. 276, pl. 8. fig. 26.

" " Heron-Allen &amp; Earland, 1914-15, FKA. p. 684.

Rare and not large, but otherwise characteristic.

137. *SPIRILLINA DECORATA Brady.**Spirillina decorata* Brady, 1884, FC. p. 633, pl. 85. figs. 22-25.

" " Heron-Allen &amp; Earland, 1914-15, FKA. p. 685.

Very rare and small.

138. *SPIRILLINA DECORATA*, var. *UNILATERA Chapman.**Spirillina decorata*, var. *unilatera* Chapman, 1901, etc., FFA. 1902, p. 410, pl. 36. fig. 17.

A single specimen, exactly resembling Chapman's figure.

139. *SPIRILLINA CAMPANULA*, sp. nov. (Pl. 36. figs. 33-41.)

Test minute, thin-walled, free or sessile, campanulate or bell-shaped, but more or less laterally compressed, the apex of the bell obtusely rounded. The exterior surface of the test, viewed as an opaque object, is dull, and the sutural lines are flush and only visible as internal markings. Viewed as a transparent object under a high power, the surface is slightly rough or scaly, and the interior of the bell is filled almost to the rim with an unseptate tube, which, starting from a rather large prolocodum occupying the apex of the bell, is coiled in 3-5 convolutions round a solid central axis or *columella*. Viewed from the base of the bell, the umbilicus is solid, smooth, and rather

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\* This paper is variously referred to as being dated 1849 and 1850. It was read in May 1849, and all the separate copies were dated on a special title-page 1849, but the volume of which it forms part was issued in 1850, and is so dated.

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- F. 1899, RFA. J. M. FLINT.—Recent Foraminifera. A Descriptive Catalogue of Specimens dredged by the U.S. Fish Commission Steamer 'Albatross,' Washington, U.S.A., 1899.
- F. 1905, SOM. C. FORNASINI.—Illustrazione di Specie Orbignyane di Miliolidi istituite nel 1826. Mem. Ac. Sci. Ist. Bologna, ser. 6, vol. ii. pp. 59-70.

Common, and presenting all the usual modifications of biconvexity. The specimens are for the most part strongly developed. No specimens of the tuberculate varieties, so abundant in some tropical gatherings, were seen.

197. *AMPHISTEGINA LESSONII*, var. *GIBBA* d'Orbigny.

*Amphistegina gibba* d'Orbigny, 1826, TMC. p. 304, no. 6.

„ *mamillata* d'Orbigny, 1846, FFV. p. 208, pl. 12. figs. 6-8.

„ *lessonii*, var. *gibba* Heron-Allen & Earland, 1914-15, FKA. p. 737.

This variety is fairly frequent and typical. It is characterized by its marked plano-convexity.

*OPERCULINA* d'Orbigny.

198. *OPERCULINA COMPLANATA* (Defrance).

*Lenticulites complanata* Defrance, 1822, Diet. Sci. Nat. vol. xxv. p. 453.

*Operculina* „ d'Orbigny, 1826, TMC. p. 281, no. 1, pl. 4. figs. 7-10; Modèle, no. 80.

„ „ Brady, 1884, FC. p. 743, pl. 112. figs. 3-5, 8.

„ „ Heron Allen & Earland, 1914-15, FKA. p. 737.

Extremely rare; represented by two moderate-sized water-worn specimens and one very minute individual. The rarity of this form is noteworthy.

*HETEROSTEGINA* d'Orbigny.

199. *HETEROSTEGINA DEPRESSA* d'Orbigny.

*Heterostegina depressa* d'Orbigny, 1826, TMC. p. 305, pl. 17. figs. 5-7; Modèle, no. 99.

„ „ Brady, 1884, FC. p. 746, pl. 112. figs. 14-20.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 738.

Rare, but large and well-developed.

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190. *NONIONINA UMBILICATULA* (Montagu).

*Nautilus umbilicatus* Montagu, 1803, TB. p. 191; Suppl. p. 78, pl. 18.  
fig. 1.

*Nonionina umbilicatus* Brady, 1884, FC. p. 726, pl. 109. figs. 8, 9.

" " Heron-Allen & Earland, 1914-15, FKA. p. 730.

A single small specimen.

191. *NONIONINA PAUPERATA* Balkwill & Wright.

*Nonionina pauperata* Balkwill & Wright, 1885, DIS. p. 353, pl. 13. figs. 25, 26.

" " Heron-Allen & Earland, 1908, etc., SB. 1911, p. 342,  
pl. 11. figs. 16, 17; 1914-15, FKA. p. 732.

Frequent and typical.

*POLYSTOMELLA Lamarck.*192. *POLYSTOMELLA STRIATO-PUNCTATA* (Fichtel & Moll).

*Nautilus striato-punctatus* Fichtel & Moll, 1798, TM. p. 61, pl. 9. figs. a-c.

*Polystomella striato-punctata* Brady, 1884, FC. p. 733, pl. 109. figs. 22, 23.

" " Heron-Allen & Earland, 1914-15, FKA. p. 733.

A single small but typical specimen.

193. *POLYSTOMELLA CRISPA* (Linné).

*Nautilus crispus* Linné, 1788, p. 3370, no. 3.

*Polystomella crista* Brady, 1884, FC. p. 736, pl. 110. figs. 6, 7.

" " Heron-Allen & Earland, 1914-15, FKA. p. 733.

Not uncommon, but small and weakly developed.

194. *POLYSTOMELLA MACELLA* (Fichtel & Moll).

*Nautilus macellus* Fichtel & Moll, 1798, TM. p. 66, pl. 10. figs. e-g.

*Polystomella macella* Brady, 1884, FC. p. 737, pl. 110. figs. 8, 9, 11.

" " Heron-Allen & Earland, 1914-15, FKA. p. 734.

Frequent and typical.

195. *POLYSTOMELLA MILLETTI* Heron-Allen & Earland.

? *Polystomella verriculata* Millett, 1898, etc., FM. 1904, p. 604, pl. 11. fig. 3.

" *milletti* Heron-Allen & Earland, 1914-15, FKA. p. 735, pl. 53.  
figs. 38-42.

A single small and starved but unmistakable specimen.

## Sub-family NUMMULITINÆ.

*AMPHISTEGINA d'Orbigny.*196. *AMPHISTEGINA LESSONII* d'Orbigny.

*Amphistegina lessonii* d'Orbigny, 1826, TMC. p. 304, no. 3, pl. 17. figs. 1-4;  
Modèle, no. 98.

" " Brady, 1884, FC. p. 740, pl. 111. figs. 1-7.

" " Heron-Allen & Earland, 1914-15, FKA. p. 736.

juxtaposed groups. The finer material provided an abundant supply of immature specimens, which when mounted in balsam exhibited a large primordial chamber with chitinous lining, followed by a single coil of about twelve globular chambers of gradually increasing size, in one plane. The chambers in the convolution are separated by dense, solid shell-substance. On completion of rather more than a single convolution, the chambers become less spherical and are irregularly heaped over their predecessors as in *Gypsina*. The spinous processes, perforated by secondary canals, are seen to originate from a solid layer of shell-substance on the outer wall of the primary coil. The general colour of the specimen is much less conspicuous than in most "Tinoporus gatherings" which have been examined. The species generally gives a yellowish-orange tint to the sands in which it is predominant, but the Lord Howe specimens are nearly white.

The complicated synonymy of this organism is fully discussed in the papers quoted above, and in others referred to in those papers.

#### POLYTREMA *Risso*.

##### 187. POLYTREMA MINIACEUM (*Pallas*).

*Millepora miniacea* Pallas, 1766, *Elenchus Zoophytorum*, p. 251.

*Polytrema miniaceum* Brady, 1884, FC. p. 721, pl. 100, figs. 5-9; pl. 101, fig. 1.

" " Heron-Allen & Earland, 1922, TN. p. 221, pl. 8; 1922, FGA. p. 139, pl. 2 (numbered 1).

Curiously rare. The specimens call for no particular comment. A few specimens of the free early stage were observed.

##### 188. POLYTREMA MINIACEUM, var. ALBA *Carter*.

*Polytrema miniaceum*, var. *album* Carter, 1877, CB. p. 213, pl. 13, figs. 14, 15.

" " „ *alba* Brady, 1884, FC. p. 721, pl. 101, figs. 2, 3.

" " „ „ Heron-Allen & Earland, 1922, TN. 226.

As usual, rarer than the type, but unmistakable.

### Family NUMMULINIDÆ.

#### Sub-family POLYSTOMELLINÆ.

##### NONIONINA *d'Orbigny*.

##### 189. NONIONINA DEPRESSULA (*Walker & Jacob*).

*Nautilus depressulus* Walker & Jacob, 1798, AEM. p. 641, pl. 14, fig. 33.

*Nonionina depressula* Brady, 1884, FC. p. 725, pl. 109, figs. 6, 7.

" " Heron-Allen & Earland, 1914-15, FKA. p. 730.

Very rare and minute.

chambers often running in irregular chains, thick-walled, coarsely perforate, but without exogenous shell-matter, colour inclined to pale red running to dirty white. The final chamber of an extended series is often subglobular in shape and of large size.

The first variety suggests *Holocladina pustulifera* Carter (C. 1880, SGM. p. 447, pl. 18, figs. 4, a-g), but lacks the terminal perforation of the spine, upon which Carter lays a stress which appears to us to be superfluous.

183. *GYPSINA RUBRA* (d'Orbigny).

*Planorbulina rubra* d'Orbigny, 1826, TMC. p. 280, no. 4.

" " Fornasini, 1908, SON. p. 44, pl. 2. fig. 3.

*Gypsina* " Heron-Allen & Earland, 1914-15, FKA. p. 725, pl. 53. figs. 35-37.

Many large fragments. The exogenous shell-growth is not so abnormally developed as is usually the case in this form.

184. *GYPSINA VESICULARIS* (Parker & Jones).

*Orbitolina vesicularis* Parker & Jones, 1859, etc., NF. 1860, p. 31, no. 5.

*Gypsina* " Brady, 1884, FC. p. 718, pl. 101. figs. 9-12.

" " Heron-Allen & Earland, 1914-15, FKA. p. 726.

A few large water-worn specimens.

185. *GYPSINA GLOBULUS* (Reuss).

*Cerriopora globulus* Reuss, 1847, Haidinger's Naturw. Abh. vol. ii. p. 33, pl. 5. fig. 7.

*Gypsina* " Brady, 1884, FC. p. 717, pl. 101. fig. 8.

" " Heron-Allen & Earland, 1914-15, FKA. p. 727.

Large, but infrequent.

BACULOGYPSINA Sacco.

186. *BACULOGYPSINA SPHÆRULATA* (Parker & Jones). (Pl. 37. fig. 65.)

*Orbitolina sphærulata* Parker & Jones, 1859, etc., NF. 1860, p. 33.

*Tinoporos baculatus* Carpenter, 1856, etc., RF. 1860, p. 564, pl. 18, figs. 2-6.

" " Brady, 1884, FC. p. 716, pl. 101. figs. 4-7.

*Baculogypsina baculata* Silvestri, 1905, B. p. 69, fig. 2.

" *sphærulatus* Cushman, 1921, FP. p. 359, pl. 75. fig. 6.

Extremely abundant; attaining large dimensions and exhibiting great variety in the number, arrangement, and development of the spines or lobose processes. These frequently have a furcate appearance, but minute examination shows that this appearance is due to the close proximity of separate processes. Some of the specimens are almost spherical, and in these, as a rule, the processes are short and inconspicuous, though often occurring in greater numbers than usual, and occasionally concentrated into closely



Very rare. This is the type with the sunken umbilicus and pronounced sutures as contrasted with the smooth and rounded type *P. micheliniana*. We have gone into this matter on several occasions, and particularly *ut supra*.

179. *PULVINULINA ELEGANS* (d'Orbigny).

*Rotalia (Turbinulina) elegans* d'Orbigny, 1826, TMC. p. 276, no. 54.

*Pulvinulina elegans* Brady, 1884, FC. p. 699, pl. 105, figs. 4-6.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 717.

One small and broken specimen.

*ROTALIA Lamarck.*

180. *ROTALIA BECCARII* (Linné).

*Nautilus beccarii* Linné, 1767, SN. p. 1162; 1788, SN. p. 3370.

*Rotalia (Turbinulina) beccarii* d'Orbigny, 1826, TMC. p. 275, no. 42; Modèle, no. 74.

„ *beccarii* Brady, 1884, FC. p. 704, pl. 107. figs. 2, 3.

One large but very weak specimen, hardly separable from the next species.

181. *ROTALIA PERLUCIDA* Heron-Allen & Earland.

*Rotalia beccarii* (pars) Balkwill & Wright, 1885, DIS. p. 351.

„ *perlucida* Heron-Allen & Earland, 1913, CI. p. 139, pl. 13, figs. 7-9; 1914-15, FKA. p. 718.

Not uncommon. Extremely depressed and pauperate.

Sub-family TINOPORINÆ.

*GYPSINA Carter.*

182. *GYPSINA INHÆRENS* (Schultze). (Pl. 37. figs. 62-64.)

*Acervulina inhærens* Schultze, 1854, OP. p. 68, pl. 6. fig. 12.

*Gypsina* „ Brady, 1884, FC. p. 718, pl. 102. figs. 1-6.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 724.

Very common, and, as usual, very variable in the size of the chamberlets. One specimen was observed characterized by the extremely small size of the constituent chambers, some of which are broken and disclose tightly packed young individuals within (fig. 62).

Among the noticeable variations are two forms: one, white with very large and loosely aggregated chambers, often extending in acervuline projections, and sometimes fairly smooth and coarsely perforate, at others covered with densely aggregated spines of secondary shell-matter. The shape may possibly be due to the irregular surface of the host from which the specimens have become detached. In another variant, possibly more nearly related to *G. rubra*, the form is wild-growing, large-chambered, the

172. *TRUNCATULINA PRÆCINCTA* Karrer.*Rotalia præcincta* Karrer, 1868, MFKB. p. 189, pl. 5. fig. 7.*Truncatulina* „ Brady, 1884, FC. p. 667, pl. 95. figs. 1-3.

„ „ Heron-Allen &amp; Earland, 1914-15, FKA. p. 709.

Very rare, but typical.

PULVINULINA *Parker & Jones.*173. *PULVINULINA REPANDA* (Fichtel & Moll).*Nautilus repandus* Fichtel & Moll, 1798, TM. p. 35, pl. 3. figs. *a-d*.*Pulvinulina repanda* Brady, 1884, FC. p. 684, pl. 104. fig. 18.

„ „ Heron-Allen &amp; Earland, 1914-15, FKA. p. 713.

Frequent and some of the specimens are large, but nearly all broken or water-worn.

174. *PULVINULINA LATERALIS* (Terquem).*Rotalina lateralis* Terquem, 1878, FIR. p. 25, pl. 2. (7) fig. 11.*Pulvinulina* „ Brady, FC. p. 689, pl. 106. figs. 2, 3.„ „ Heron-Allen & Earland, 1914-15, FKA. p. 714, pl. 53.  
figs. 6-11.

One large and typical specimen.

175. *PULVINULINA CONCENTRICA* Parker & Jones.*Pulvinulina concentrica* Parker, Jones, & Brady, 1864, RFS. p. 470, pl. 48.  
fig. 14.

„ „ Brady, 1884, FC. p. 686, pl. 105. fig. 1.

„ „ Heron-Allen &amp; Earland, 1914-15, FKA. p. 714.

Small, but frequent and typical.

176. *PULVINULINA CANARIENSIS* (d'Orbigny).*Rotalina canariensis* d'Orbigny, 1839, FIC. p. 130, pl. 1. figs. 34-36.*Pulvinulina* „ Brady, 1884, FC. p. 692, pl. 103. figs. 8-9.

„ „ Cushman, 1921, FP. p. 338, pl. 66. fig. 1.

Rare, but quite typical.

177. *PULVINULINA CRASSA* (d'Orbigny).*Rotalina crassa* d'Orbigny, 1840, CBP. p. 32, pl. 3. figs. 7, 8.*Pulvinulina* „ Brady, 1884, FC. p. 694, pl. 103. figs. 11, 12.

„ „ Cushman, 1921, FP. p. 338, pl. 67. fig. 3.

Frequent and well-developed.

178. *PULVINULINA TRUNCATULINOIDES* (d'Orbigny).*Rotalina truncatulinoides* d'Orbigny, 1839, FIC. p. 132, pl. 2. figs. 25-27.*Pulvinulina* „ Heron-Allen & Earland, 1922, TN. p. 216.

PLANORBULINA *d'Orbigny*.166. PLANORBULINA MEDITERRANEANSIS *d'Orbigny*.

*Planorbulina mediterraneensis* d'Orbigny, 1826, TMC. p. 280, pl. 14. figs. 4-6;  
Modèle, no. 79.

" " Brady, 1884, FC. p. 656, pl. 92. figs. 1-3.

" " Heron-Allen & Earland, 1914-15, FKA. p. 705.

A single large specimen.

167. PLANORBULINA LARVATA *Parker & Jones*.

*Planorbulina vulgaris*, var. *larvata* Parker & Jones, 1859, etc., NF. 1860,  
p. 294.

" *larvata* Brady, 1884, FC. p. 658, pl. 92. figs. 5, 6.

" " Heron-Allen & Earland, 1914-15, FKA. p. 706.

One somewhat doubtful specimen.

TRUNCATULINA *d'Orbigny*.168. TRUNCATULINA LOBATULA (*Walker & Jacob*).

*Nautilus lobatulus* Walker & Jacob, 1798, AEM. p. 642, pl. 14. fig. 35.

*Truncatulina lobatula* Brady, 1884, FC. p. 660, pl. 92. fig. 10 (etc.).

" " Heron-Allen & Earland, 1914-15, FKA. p. 706.

Common and presenting the usual range of variation.

169. TRUNCATULINA VARIABILIS *d'Orbigny*.

*Truncatulina variabilis* d'Orbigny, 1826, TMC. p. 279, no. 8.

" " Brady, 1884, FC. p. 661, pl. 93. figs. 6, 7.

" " Heron-Allen & Earland, 1914-15, FKA. p. 706; 1922,  
FGA. p. 137, pl. 1 (numbered 2). figs. 38, 39.

Very common, ranging from normal variations up to the wild-growing Soldanian types.

170. TRUNCATULINA REFULGENS (*Montfort*).

*Oibicides refulgens* Montfort, 1808-10, CS. vol. i. p. 122, 31<sup>me</sup> genre.

*Truncatulina* " Brady, 1884, FC. p. 659, pl. 92. figs. 7-9

" " Heron-Allen & Earland, 1914-15, FKA. p. 707.

Very common and highly typical.

171. TRUNCATULINA UNGERIANA (*d'Orbigny*).

*Rotalina ungeriana* d'Orbigny, 1846, FFV. p. 157, pl. 8. figs. 16-18.

*Truncatulina* " Brady, 1884, FC. p. 664, pl. 94. fig. 9.

" " Heron-Allen & Earland, 1914-15, FKA. p. 708.

Frequent and well-developed.

is moderately common in the material, as it is, indeed, in shallow-water gatherings from most tropical and temperate seas. Liebus and Schubert's variety, *D. tabernacularis*, var. *levis* (Jahrb. k.-k. geol. Reichsanst. 1902, vol. lii. p. 301, fig. 5), has many points of resemblance, but differs in the absence of the characteristic radial beading which decorates the base of *D. lauriei*, as it does the base of *D. tabernacularis*.

165. *DISCORBINA PYRAMIDALIS*, sp. nov. (Pl. 37. figs. 56-61.)

Test free, shaped like a four-sided pyramid with slightly excavated sides, and salient angles, consisting of 3-5 convolutions, each of four chambers, the widest portion of each chamber being at the angle, and the sutural divisions running down the middle of each side. Shell-wall thick; the base excavate, studded with beads, arranged radially, with the aperture of the final chamber in the umbilical recess. In all the specimens examined in balsam the primordial chamber is large and spherical, occupying as much as a quarter of the pointed apex of the pyramid.

Several "twinned" pairs occur. The specimens are usually about the same size. There is a considerable range both in size and height of the free individuals; in fact, there appear to be two fairly distinctive forms, one small and more or less regularly pyramidal (*i. e.*, the height being roughly equal to the diameter of the base), the other with a height double that diameter. These may represent the megal- and microspheric stages of the organism. Among other variations noticeable are (1) a single three-sided specimen, (2) several specimens in which the angular edges of the pyramid are curving lines, so that, when viewed from the top, a spiral structure is suggested. The shell is thick and free from surface ornamentation.

This species is evidently closely allied to Millett's *D. corrugata* (M. 1898, etc., FM. 1903, p. 700, pl. 7. fig. 5). We have good examples of this, from the Arakan coast of Burma<sup>1</sup>. Millett's original types, which are in our possession, bear, in his handwriting, as locality "Sagami Bay, Japan." Millett's form has five salient angles and a much less polished exterior than *D. pyramidalis*. We have typical specimens of *D. pyramidalis* from Suva, Fiji Is. (12 fms., very rare), and we have noted its occurrence at 'Challenger' Station 185, "Raine Id." (155 fms., also very rare), so that we may assume that the form is widely distributed in the tropical Pacific. It is of constant occurrence in a series of shore-sands which we possess from St. Vincent's Gulf and Spencer Gulf (S. Australia), and it also occurs in two shore-sands from W. Australia (Fremantle and Rottnest Island). The lack of suitable material from the remaining shores of Australia renders the records incomplete, but it appears highly probable that the species will be found to be a typical form in Australian shore-gatherings.

Size. Basal diameter at edges .08-16 mm. (small type) to .28 mm. (large type). Height .05-21 mm. (small type) to .35 mm. (large type).

160. *DISCORBINA PULVINATA* Brady. (Pl. 36. figs. 42-46.)*Discorbina pulvinata* Brady, 1884, FC. p. 650, pl. 88. figs. 10, a, b.

" " Sidebottom, 1904, etc., RFD. 1908, p. 14, pl. 5. fig. 4.

" " Heron-Allen &amp; Earland, 1914-15, FKA. p. 703.

Frequent, and the specimens vary between relatively smooth and highly corrugate on the superior face: Nearly all of them exhibit "budding" in various stages, from a single minute primordial chamber in the umbilicus of the oral side to specimens in which the base and internal septa have disappeared by absorption. Two individuals with young brood clustered round the orifice were observed, which we figure.

161. *DISCORBINA PATELLIFORMIS* Brady.*Discorbina patelliformis* Brady, 1884, FC. p. 647, pl. 88. fig. 3; pl. 89. fig. 4.

" " Sidebottom, 1904, etc., RFD. 1908, p. 14, pl. 5. fig. 3.

" " Heron-Allen &amp; Earland, 1914-15, FKA. p. 703, pl. 52. fig. 32.

Very common and attaining a large size. The specimens are perfectly preserved and very handsome. One "budding" pair of small individuals was observed.

162. *DISCORBINA HARMERI* Heron-Allen & Earland.*Discorbina harmeri* Heron-Allen & Earland, 1922, TN. p. 204, pl. 7. figs. 9-11.

One minute but typical specimen. It is interesting to note the occurrence of this recently described species in a new area, though it is evidently not firmly established there.

163. *DISCORBINA TABERNACULARIS* Brady. (Pl. 36. figs. 47-49.)*Discorbina tabernacularis* Brady, 1884, FC. p. 648, pl. 89. figs. 5-7.

" " Heron-Allen &amp; Earland, 1914-15, FKA. p. 704.

Common and quite typical. Many "budding" and associated pairs; also individuals with the base and septa eroded. A specimen of the latter where the internal cavity was filled with young individuals (fig. 49).

164. *DISCORBINA LAURIEI*, nom. nov. (Pl. 36. figs. 50-52; Pl. 37. figs. 53-55.)*Discorbina tabernacularis* Sidebottom, 1910, RFBP. p. 25, pl. 3. fig. 12.

The little test figured by Sidebottom though doubtless allied to *D. tabernacularis* cannot be taxonomically referred to that species. It has many points of distinction: the paucity of chambers, which rarely exceed two convolutions of five chambers each; its blunted, or rounded, apex, with a prominent primordial chamber; its greatly inferior but constant size; and perhaps, most of all, its constant habit of "budding" pairs. Specimens which do not present this feature are so uncommon as to be noticeable. It

154. *DISCORBINA VALVULATA* (d'Orbigny).

*Rosalina valvulata* d'Orbigny, 1826, TMC. p. 271, no. 4; 1836, FIC. p. 136, pl. 2. figs. 19-21.

*Discorbina* .. Brady, 1884, FC. p. 644, pl. 87. figs. 5-7.

.. .. Heron-Allen & Earland, 1914-15, FKA. p. 695.

Common. Very fine and typical specimens.

155. *DISCORBINA RENIFORMIS* Heron-Allen & Earland.

*Discorbina reniformis* Heron-Allen & Earland, 1914-15, FKA. p. 698, pl. 52. figs. 7-14.

A single quite characteristic specimen of this very obscure species. It appears to be very widely distributed over the Indo-Pacific area, though it is always rare.

156. *DISCORBINA RUGOSA* (d'Orbigny).

*Rosalina rugosa* d'Orbigny, 1839, FAM. p. 42, pl. 2. figs. 12-14.

*Discorbina* .. Brady, 1884, FC. p. 652, pl. 87. fig. 3; pl. 91. fig. 4.

.. .. Heron-Allen & Earland, 1914-15, FKA. p. 197.

Rare, but very fine and typical specimens.

157. *DISCORBINA POLYSTOMELLOIDES* Parker & Jones.

*Discorbina polystomelloides* Parker & Jones, 1865, NAAF. p. 421, pl. 19. fig. 8.

.. .. Brady, 1884, FC. p. 652, pl. 91. fig. 1.

.. .. Heron-Allen & Earland, 1914-15, FKA. p. 698, pl. 52. figs. 19-23.

Common and attaining comparatively enormous dimensions, the largest having a maximum diameter of 3 mm. The specimens vary considerably in their surface ornament, some having developed secondary shell-structure in the form of beads and ribs to an extent that we have never previously observed in this species.

158. *DISCORBINA RIMOSA* Parker & Jones.

*Discorbina rimosa* Carpenter, Parker, & Jones, 1862, ISF. p. 205.

.. .. Millett, 1898, etc., FM. 1903, p. 702, pl. 7. fig. 7.

.. .. Heron-Allen & Earland, 1914-15, FKA. p. 700.

The specimens referable to this species merely tend to confirm our views expressed (*ut supra*) as to the inexpediency of separating this species from *D. polystomelloides*. They could very well be included as pauperate specimens of the latter, in view of the wide range of variation exhibited by that species.

159. *DISCORBINA RARESCENS* Brady.

*Discorbina rarescens* Brady, 1884, FC. p. 651, pl. 90. figs. 2, 3, & ? 4.

.. .. Heron-Allen & Earland, 1914-15, FKA. p. 700.

One small but perfectly typical specimen.

147. *DISCORBINA VILARDEBOANA* (*d'Orbigny*).*Rosalina vilardeboana* d'Orbigny, 1839, FAM. p. 44, pl. 6. figs. 13-15.

" " Brady, 1884, FC. p. 645, pl. 86. fig. 12; pl. 88. fig. 2.

" " Heron-Allen &amp; Earland, 1914-15, FKA. p. 692.

Frequent and generally small, but some of the specimens attained very large size.

148. *DISCORBINA ROSACEA* (*d'Orbigny*).*Rotalina rosacea* d'Orbigny, 1826, TMC. p. 273, no. 15; Modèle, no. 39.*Discorbina* " Brady, 1884, FC. p. 644, pl. 87. figs. 1, 4.

" " Heron-Allen &amp; Earland, 1914-15, FKA. p. 692.

Frequent and typical.

149. *DISCORBINA BACCATA* *Heron-Allen & Earland*.*Discorbina baccata* Heron-Allen & Earland, 1913, CI. p. 124, pl. 12. figs. 1-3; 1922, TN. p. 200.

A single small but typical specimen.

150. *DISCORBINA TURBO* (*d'Orbigny*).*Rotalia (Trochulina) turbo* d'Orbigny, 1826, TMC. p. 274, no. 39; Modèle, no. 73.*Discorbina turbo* Brady, 1884, FC. p. 642, pl. 87. fig. 8.

" " Heron-Allen &amp; Earland, 1914-15, FKA. p. 693.

A single small specimen.

151. *DISCORBINA MEDITERRANENSIS* (*d'Orbigny*).*Rosalina mediterraneensis* d'Orbigny, 1826, TMC. p. 271, no. 2.*Discorbina* " Heron-Allen & Earland, 1913, CI. p. 118, pl. 9. figs. 12-14, pl. 10. fig. 1; 1914-15, FKA. p. 693.

Common and very typical.

152. *DISCORBINA GLOBULARIS* (*d'Orbigny*).*Rosalina globularis* d'Orbigny, 1826, TMC. p. 271, no. 1, pl. 13. figs. 1-4; Modèle, no. 69.*Discorbina* " Brady, 1884, FC. p. 643, pl. 86. figs. 8, 13.

" " Heron-Allen &amp; Earland, 1914-15, FKA. p. 694, pl. 51. figs. 36-39.

Very common, presenting every range of variation from depressed forms hardly separable from *D. cora* to highly inflated specimens separable only from *D. valvulata* by the absence of limbation.

153. *DISCORBINA ARAUCANA* (*d'Orbigny*).*Rosalina araucana* d'Orbigny, 1839, FAM. p. 44, pl. 6. figs. 16-18.*Discorbina araucana* Brady, 1884, FC. p. 645, pl. 86. figs. 10, 11.

" " Heron-Allen &amp; Earland, 1914-15, FKA. p. 695.

Common and fairly typical, varying considerably in size.

CYMBALOPORA *Hagenow*.141. CYMBALOPORA POEYI (*d'Orbigny*).

*Rosalina poeyi* d'Orbigny, 1839, FC. p. 92, pl. 3. figs. 18-20. *Rotalia squamosa*, p. 91, pl. 3. figs. 12-14.

*Cymbalopora poeyi* Brady, 1884, FC. p. 636, pl. 102. fig. 13.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 687.

One small and weak, and one large and typical specimen.

142. CYMBALOPORA MILLETTII *Heron-Allen & Earland*.

*Cymbalopora bulloides* Millett, 1898, etc., FM. 1903, p. 697, pl. 7. fig. 4.

„ *millettii* Heron-Allen & Earland, 1915, FKA. p. 689, pl. 51. figs. 32-35.

„ „ Heron-Allen, 1915, RPF. p. 253, pl. 16. fig. 36; pl. 17. figs. 46-48, 50, 51.

One perfect specimen with the characteristically marked balloon, and a number of specimens of the apical rotaline mass of chambers.

DISCORBINA *Parker & Jones*.143. DISCORBINA CORA (*d'Orbigny*).

*Rosalina cora* d'Orbigny, 1839, FAM. p. 45, pl. 6. figs. 19-21.

„ „ Heron-Allen & Earland, 1915, FKA. p. 690; 1922, FGA. p. 133, pl. 1 (numbered 2). figs. 33-35.

Fairly typical examples of this very primitive form of *D. globularis* occur, but they are rare.

144. DISCORBINA NITIDA (*Williamson*).

*Rotalina nitida* Williamson, 1858, RFGB. p. 54, pl. 4. figs. 106-108.

*Rotalia* „ Brady, 1884, FC. p. 627.

*Discorbina* „ Heron-Allen & Earland, 1914-15, FKA. p. 691.

Very rare, minute and weak.

145. DISCORBINA CONCINNA *Brady*.

*Discorbina concinna* Brady, 1884, FC. p. 646, pl. 90. figs. 7, 8.

„ „ Egger, 1893, FG. p. 388, pl. 15. figs. 22-24.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 691.

Frequent and typical.

146. DISCORBINA ISABELLEANA (*d'Orbigny*).

*Rosalina isabelleana* d'Orbigny, 1839, FAM. p. 43, pl. 6. figs. 10-12.

*Discorbina* „ Brady, 1884, FC. p. 646, pl. 88. fig. 1.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 692.

Frequent. The specimens are good, but small.



deeply depressed, showing no sign of coiling or of an oral aperture. As in *Spirillina lucida* Sidebottom, the oral extremity of the tube is compressed and sealed into the outer wall of the test. The protoplasmic body, which is dark yellow in colour and full of minute granules of darker tint, is voluminous and occupies the whole of the convolutions.

*Spirillina campanula* is interesting as presenting an entirely novel plan of growth. The genus is normally a plano-spirally coiled tube, but in most of the species a certain degree of asymmetry is observable between the two faces of the spire, one being raised and the other depressed. This tendency is particularly noticeable in *S. revertens* Rhumbler and *S. lucida* Sidebottom, and is still more pronounced in *S. groomii* Chapman, but none of these can compare with the extraordinary convexity of *S. campanula*.

The species is probably abundant at Lord Howe Island, as many specimens were found in spite of the very small quantity of fine material available for examination. All the specimens were free except one, which was sessile on a fragment of coralline. The perfect manner in which the rim of the bell with its excised edges adapted itself to the shape of the host suggests that such a sessile habitat may be normal, at any rate, up to a stage in the existence of the organism. Such conditions would account for the peculiar form of the rim and the varying degree of compression of the bell. But a careful search of the small quantity of coralline available did not provide further specimens.

One large individual has lost all internal septa by absorption, and the entire cavity of the bell is packed with young individuals, each consisting of a proloculum encircled by a complete coil of tube. At least ten individuals can be counted in the cavity.

The size and relative proportions are very variable. Five specimens measured for height and maximum breadth gave the following measurements:—

Height .....	·15	·075	·15	·095	·115 mm.
Breadth .....	·187	·125	·162	·125	·125 mm.

Four others measured gave:—

Maximum breadth.....	·135	·1	·11	·095 mm.
Thickness at rim .....	·107	·08	·087	·08 mm.

#### Sub-family ROTALINÆ.

##### PATELLINA *Williamson*.

#### 140. PATELLINA CORRUGATA *Williamson*.

*Patellina corrugata* Williamson, 1858, RFGB. p. 46, pl. 3. figs. 86-89.

„ „ Brady, 1884, FC. p. 634, pl. 86. figs. 1-7.

„ „ Heron-Allen & Earland, 1914-15, FKA. p. 687.

Common and typical. All of the rather low-domed, scaly type.

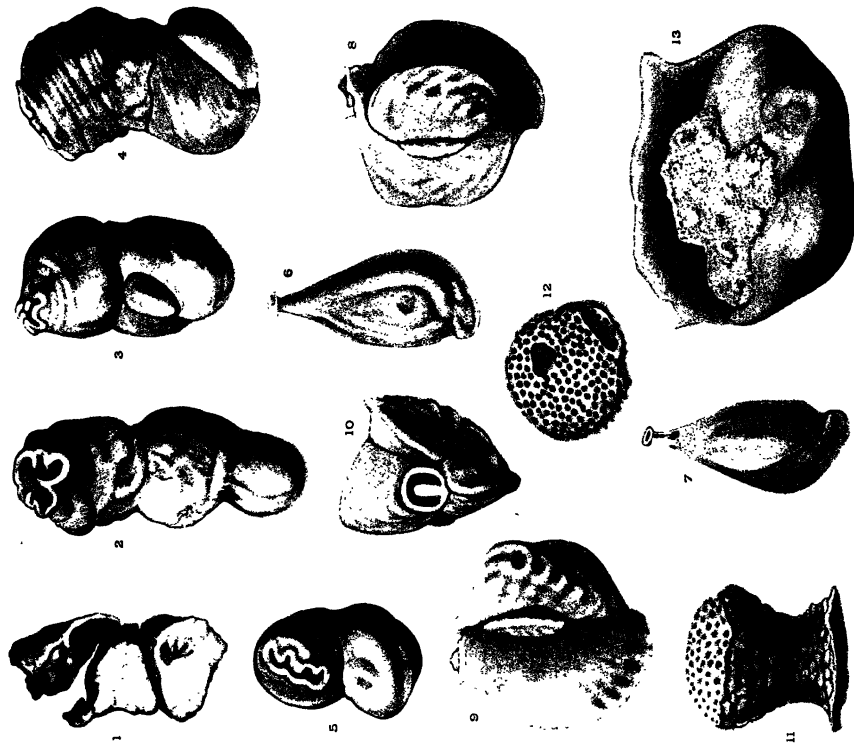
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## EXPLANATION OF THE PLATES.

## PLATES 35-37.

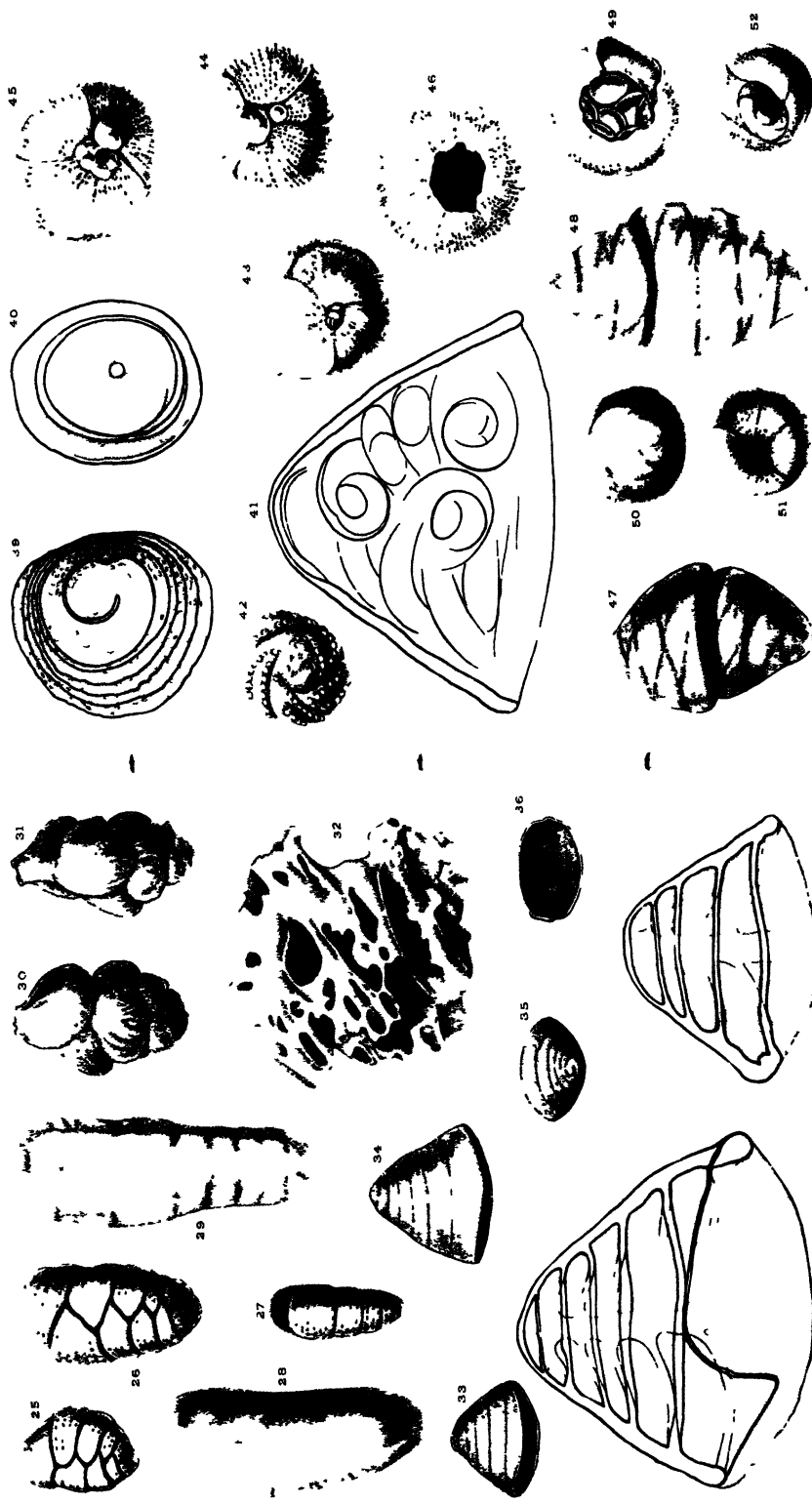
- Fig. 1. *Nubecularia lucifuga* DeFrance. Showing young individuals in fractured chamber.  $\times 55$ .
- 2-5. " *schauslandi* (Rhumbler).  $\times 35$ .
- 6-7. *Spiroloculina tenuirostra* Karrer. Fig. 6. Central portion abraded.  $\times 145$ .
8. *Miliolina auberiana*, var. *semireticulata*, var. nov. Front view. }  $\times 55$ .
9. " " " " Back view. }
10. " " " " Oral view. }
11. *Craterites rectus*, gen. nov. et sp. nov. Side view, showing the expanding base, layers of chamberlets, and cribrate oral surface.  $\times 30$ .
12. " " gen. nov. et sp. nov. Superior view of cribrate oral surface, showing similar structure underneath through fractures on surface-layer.  $\times 30$ .
13. *Diffusilina humilis*, gen. nov. et sp. nov. A perfect specimen attached to Nullipore, showing pustular processes on the surface, which is otherwise un-abraded.  $\times 28$ .
- 14-16. " " gen. nov. et sp. nov. Specimens showing partially abraded surface, exposing the labyrinthic protoplasmic structure (shown black).  $\times 28$ .
17. *Haddonina torrensis* Chapman. Young textularian specimen, showing commencement of wild later growth.  $\times 30$ .
- 19-20. " " " Fully-developed specimens, showing textularian commencement to wild-growing portion.  $\times 30$ .
21. " " " Showing the oral extremity.  $\times 30$ .
- 18 & 22. " " " Specimens incorporating large sand-grains.  $\times 30$ .
- 23-24. *Bulimina elegantissima* d'Orbigny. Fig. 23. The bud is a single chamber; Fig. 24, developed into a young individual of several chambers.  $\times 145$ .
- 25-26. *Bolivina limbata*, var. *abbreviata*, nov. Side views. }  $\times 145$ .
27. " " " " Edge view. }
28. *Fronicularia scottii* Heron-Allen & Earland. Specimen from Lord Howe Island.  $\times 145$ .
29. " " " " Specimen from 'Challenger' Stn. 185 (Raine Island).  $\times 145$ .
- 30-31. *Unigeringina selasyensis* Heron-Allen & Earland.  $\times 145$ .
32. *Ramulina grimaldii* Schlumberger.  $\times 28$ .
- 33-34. *Spirillina campanula*, sp. nov. Side views. } Viewed as opaque specimens.
35. " " " Apical view. }
36. " " " Basal view. }
- 37-38. " " " Balsam mounts. Side views.
39. " " " " " Apical view. Scaly surface.
40. " " " " " Basal view.
41. " " " " " Specimen in which the septa having been entirely absorbed, the central cavity is filled with a mass of young individuals, which are shown in optical section. All  $\times 340$ .
42. *Discorbina pulvinata* Brady. Superior view.
- 43-45. " " " Basal view, showing development of young individuals around oral aperture.





FORAMINIFERA FROM

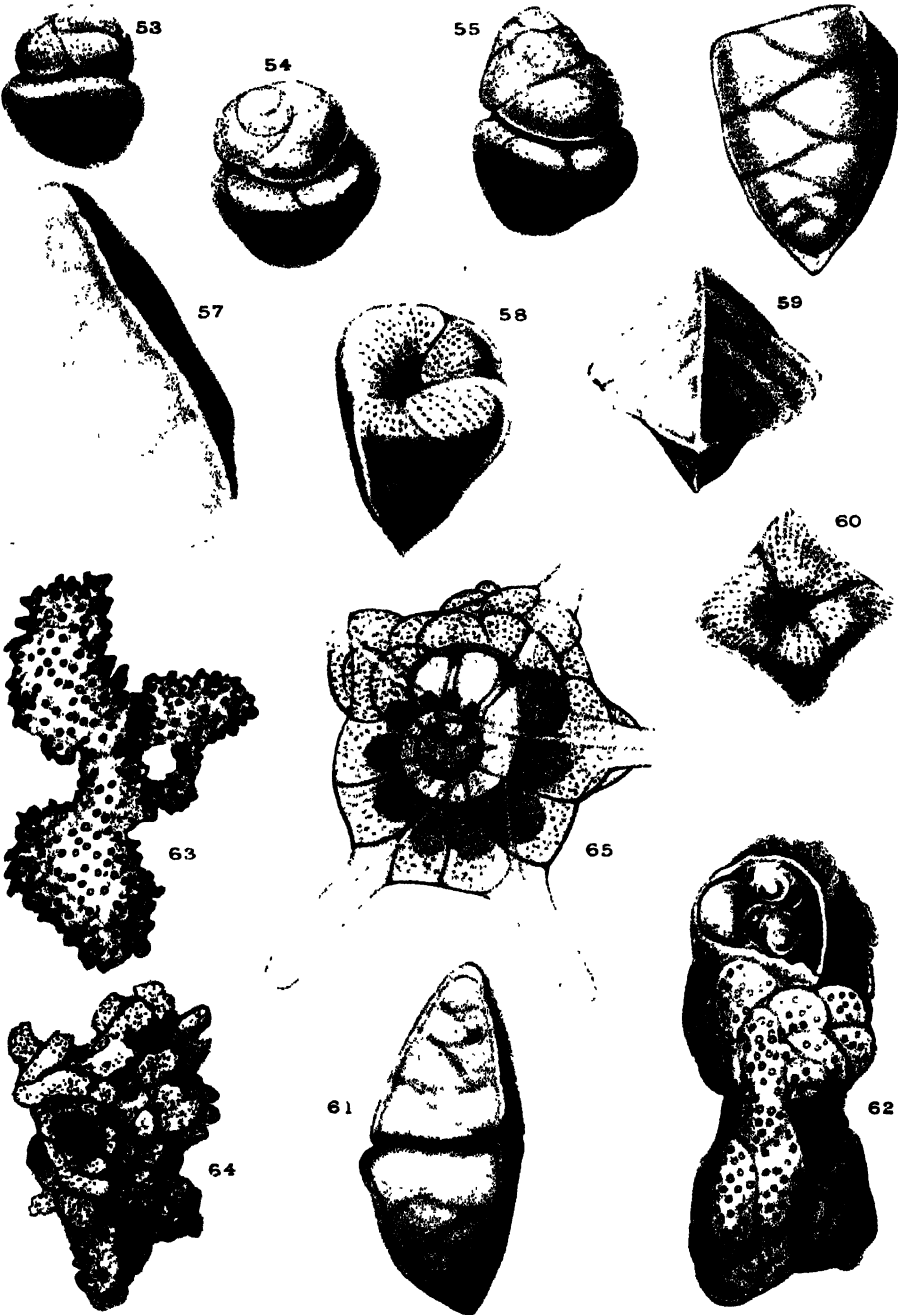
LORD HOWE ISLAND



FORAMINIFERA FROM LORD HOWE ISLAND

FORAMINIFERA FROM LORD HOWE ISLAND





FORAMINIFERA FROM LORD HOWE ISLAND





- Fig. 46. *Discorbina pulvinata* Brady. Basal view of specimen in which the internal septa and central portion of the base have been absorbed after process of reproduction. All  $\times 145$ .
- 47-48. " *tabernacularis* Brady. Adult budded pairs.  $\times 145$ .
49. " " " Basal view of specimen, showing young individuals. (The marginal edge is broken away.)  $\times 145$ .
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51. " " " Basal (oral) view.
- 52-55. " " " Specimens showing budding young in various stages of development. All  $\times 145$ .
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62. *Gypsina inhaerens* Schultze. Specimen showing young individuals in broken chamber.  $\times 145$ .
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